X. *The Colour-Physiology of Higher Crustacea.*

By Frederick Keeble, *M.A., University College, Reading, and* F. W. Gamble, *D.Sc., Owens College, Manchester. Communicated by Professor* S. J. Hickson, *F.R.S.*

Received July 16, 1902,—Read November 27, 1902.

[Plates 18–23.]

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SECTION I.

INTRODUCTION.

Statement of the Problem.

THE chromatophores of Crustacea present many problems physiological and morphological. The first attempt to formulate these problems, and, by experimental methods, to solve them, is due to POUCHET. His Memoir, 'Changements de Coloration sous l'influence des nerfs,' is a classic of biological literature. It forms the basis of our present knowledge of the colour-physiology of Crustacea.

The scope of POUCHET'S work is very wide. It includes the histology of the chromatophores, the chief chemical reactions of the more common pigments, the phenomena of pigment-movement under various extrinsic stimuli, such as light, electricity and drugs, the analysis of the effective light-factor, and experimental proof of the mode of action of this factor. These investigations were carried out chiefly on *Palæmon serratus* and *Crangon vulgaris*; of other forms, young lobsters and *Hippolyte* were occasionally employed.

POUCHET regarded each chromatophore or "chromoblaste" as a single cell containing a single pigment. Associations of pigments, for example, red and yellow as in the prawn, or red, violet and yellow as in the shrimp, POUCHET regarded as due to groups of such severally pigmented cells. Change of colour he considered was due to active protrusion or retraction of cell-processes, carrying pigment outwards or inwards.

The phenomena of pigment-movement, to which POUCHET chiefly devoted his attention, were those resulting from the use of black and white dishes in broad daylight. On the black background the pigments expand, and the resultant coloration is a dark one in harmony with the tone of the surroundings. On the white background they contract, and the consequent colourless phase offers no contrast to the adjacent surfaces. This faculty of adjustment of colour to the tint of the environment, POUCHET called the "chromatic function." In the purposefulness of the reaction he saw the function of pigment, and to the cause of the reaction and to the mode of action of this cause he devoted his experiments. He showed that the chromatic function persisted only so long as the eyes of the Crustacea were intact: eye-amputated specimens becoming and remaining dark in colour, even on white backgrounds, until the eye regenerated. Then renewed sight was followed by regained chromatic function. Since the incident light on both backgrounds was the same, the effective light-component must be some quality of the background, and without further analysing this factor, and without determining how its effect was

produced on the eye, POUCHET concluded that background determined the movements of the chromatophores through the mediation of the eye and nervous system.

In view of the scope of the present paper, we may refer to the points in which our work differs from, or supplements, POUCHET'S. Whilst fully confirming POUCHET'S discovery of the paramount importance of background in determining the movement of chromatophores, we endeavour to analyse this and the other factors involved in such reactions. POUCHET overlooked the immediate and evanescent results of contrasted backgrounds. He denied the after-effect of day and night, or of other forms of stimulation, upon Crustacea. He made no attempt to determine whether "background" influenced the development of chromatophores; and except in the case of the larval shrimp, gave no account of the distribution of these structures in the Crustacea he experimented upon.

In recent years, investigators into the colour-physiology of Crustacea have confined themselves to special problems such as the phenomena of colour-change, the chemistry of the pigments, and their physiological *rôle*. JOURDAIN (1878) pointed out that in addition to light, electrical and pharmacological stimuli, the temperature of the water influenced the colour of sensitive Crustacea, and that such changes were naturally independent of the action of the retina. We showed (1900), in *Hippolyte varians*, that rapid movements in the chromatophore could be induced by any decided stimulation; that slow changes followed the application of less powerful stimuli, such, for example, as differently coloured backgrounds in place of strongly contrasted ones; and that underlying these quick and slow reactions of the chromatophores to changes of environment, there was at least one intrinsic chromatophoric rhythm, the after-effect of alternating night and day.

Another special problem offered by the movements of chromatophores is that of the changes in the retinal pigment. S. EXNER (1891) and PARKER (1897), to mention only two cases, have shown that in the eyes of Crustacea exposed to the light, the retinal pigment aggregates round the inner ends of the cones, whereas under the influence of darkness the pigment migrates towards their outer ends; and EXNER has explained how in bright and dim light the resulting pigment movements act physiologically as a contractile iris. In these, as in many other recent experiments upon the action of light upon Crustacea, the incident light alone has been considered. The result of POUCHET'S work in emphasising the importance of reflected light has been overlooked.

The chemistry of Crustacean pigments has been the subject of Memoirs by MALY (1881), MOSELEY (1879), KRUKENBERG (1882), MAC MUNN (1884), ZOPF (1892), HEIM (1892), NEWBIGIN (1896), and others. The most complete investigation is that of ZOPF on the red and yellow pigments of *Diaptomus*, a Copepod. These pigments ZOPF identifies as two forms of those widely distributed lipochromes now known as carotins, of which the colouring matter of *Daucus carota* is the type. Both the red and yellow carotins of *Diaptomus* give an absorption band, the line

h of the spectrum, but in other respects they differ widely from each other. The red carotin readily unites with alkalies and alkaline earths, gives only a single absorption band (about the F line), and probably contains oxygen in its molecular constitution. The yellow carotin does not unite with alkalies, gives the F band and also one between F and G, and according to the valuable researches of KOHL (1902), is an unsaturated hydrocarbon $C_{26}H_{38}$. The red and yellow colouring matters of higher Crustacea are probably identical with these carotins, but the constitutions of the blue, violet and brown pigments are still unknown. With respect to the functions of these pigments, we have the respiratory hypothesis of MALY (1881) and the dehydration hypothesis of HEIM (1892), but the ascertained facts of the chemistry and physiology of Crustacean pigments are as yet too slender a basis for profitable speculation on their functions.

In the present paper we endeavour to make a survey of several of the problems which the morphology and physiology of Crustacean pigments and chromatophores present. We bring forward a number of new facts and offer suggestions as to their significance, but we feel that the time has not yet come when we can profitably enter upon an exhaustive discussion of all the known phenomena of Crustacean colour-physiology. We hope, however, after a further spell of experimental and histological work to be in a position to undertake this task.

As far as we can gather, current opinions holds that the pigment of Crustacea are sporadic and superficial in distribution; that they are confined to isolated single cells, chromatophores, of the epidermis or connective tissues, and that they are "protective" in function, or form a waste functionless product of metabolism.

Our investigations of the last four years have led us to regard these opinions as founded on insufficient evidence. Even the protective function of colour is not firmly based on experimental evidence. The pigments of *Hippolyte*, *Mysis* and *Palæmon* are not sporadic, but regular in distribution. They occur not only superficially, but in relation to deep-seated tissues. They are contained not in isolated cells, but in a system of organs often multicellular and complex in structure, the different parts of which are often in actual continuity, and are in functional relation with one another, and with the eyes through the mediation of the nervous system. Whilst even if experimental evidence of the protective value of the chromatophores and their pigments is ultimately forthcoming, we yet require to know at what stage in what process the pigments have been produced.

From this it will be clear that the whole range of what we may call the pigment morphology and pigment-physiology of Crustacea has yet to be investigated. We must ask what is the nature of these chromatophores that produce and distribute the pigments? How do they and their contained pigments arise and develop during the life of these animals? How are they brought to form a system working as a whole? Is this pigmentary system formed upon a plan common to all the higher Crustacea (Schizopods and Decapods), or does it show grades of evolution in passing

from the lower to the higher forms, and from the earlier to the latter stages of individual development? If we find that the chromatophore-system is in some sense a transmissible system, we shall have to determine how far inheritance and how far environment and acquisition determine the final colour-display. Further, if we find that in a given "species" the chromatophores are not sporadic but of constant distribution, and if in allied species there are constant differences in the arrangement of the chromatophores, we shall have to ask whether the chromatophore-system itself may not provide us, *in virtue of its form*, with a convenient and reliable taxonomic guide by which the nature and affinities of species and genera may be determined.

Our experimental work has been carried out during vacation-time in several laboratories on the coasts of England (Plymouth, Piel, Cullercoats), on the coast of Normandy (St. Vaast-la-Hogue) and Brittany (Roscoff, Trégastel). During term-time we have continued the investigations at the Zoological Laboratory, Owens College, Manchester, and University College, Reading.

We beg to express our grateful thanks to the directors of these marine biological stations for their kindness in putting at our disposal the resources of their laboratories. We also wish to acknowledge a grant of £25 from the Grant Committee of the Royal Society, thanks in a large measure to which we have been able to continue our researches at Trégastel.

Our sincere thanks are also expressed to Miss D. RICHARDSON for the excellent drawings of *Mysis* and prawn-larvæ that accompany this paper (see Plates 18, 19, 20, and Plate 22, figs. 29–32).

SECTION IA.

General Features of the Chromatophore-System of Higher Crustacea.

The pigments of Schizopod Crustacea and of such Decapods as *Hippolyte* and *Palæmon* are contained in a system of organs—the chromatophore-system. The components of this system are the chromatophores. Each chromatophore consists of a centre, and of branches radiating from that centre. The centre contains one or more pigments, which pass on appropriate stimulation into the branches. In their development, the branches resemble those of a growing tree, both in repeated sub-division and increasing complexity, interlacing in *Hippolyte* to give rise to the appearance of networks. The colour and colour-patterns are due to the distribution of pigments in these branches. When appropriate stimulations recalls the pigments into the centres, colour and colour-pattern are lost; the centres are delimited.

In its earliest development, the chromatophore consists of an unbranched body. As it becomes stellate through the out-growth of branches, the pigments become functional, so that their movements may be watched even in the embryo. The

branches considered collectively pass not only to superficial but also to deep-lying tissues. The pigments flowing into the former give rise to the colour and colour-pattern. Those flowing into the latter play little or no part in coloration.

Although the chromatophores react as a whole to a given stimulus by redistribution of their pigments, yet each group of chromatophores has its own rate of response. Moreover, the pigments themselves respond at different rates.

SECTION II.

The Chromatophore-System of Macromysis Flexuosa.

(Plates 21, 22, and 23, fig. 51, and *cf.* Plates 18–21.)

The particular species or colour-form we call *Macromysis flexuosa* (see Sect. VI.) is one of the commonest Schizopods and may be used as a type, with the colour-scheme of which that of other Crustacea may be compared.

On a sandy shore, this animal appears transparent and colourless or of a greyish tint. Amid dark surroundings and in deeper water, its colour deepens and its definite pattern becomes manifest. This consists of paired arborisations of a yellow or whitish colour upon a dark brown background. They occur in each segment of the tail and less regularly on the carapace, eyes, and limbs. The females are readily distinguished from the males by the black and yellow markings of the brood-lamellæ. In other respects, the coloration of the two sexes is essentially similar, but, on the average, the females exhibit the arborescent pattern in a more luxuriant and better defined form than do the males.

The difference of coloration exhibited by *Macromysis flexuosa* according to the light or dark nature of its surroundings can be artificially induced, and it can be shown that the transparent colour-variety is due to complete retraction of both a brown pigment and of a yellow or white reflecting substance from the branches of the chromatophores to their centres; that the dark variety is the expression of the injection of these substances into the branches; and that grey, yellowish and light brown varieties are intermediate stages. We conclude that this apparent inconstancy of colour is but an expression of the varying rates of flow of the two coloured substances, and that the system in which the flow takes place is itself unchanged.

A. *The Chromatophore-centres.*

The chromatophore-centres consist of three main groups and of one accessory group. The main groups are :—

1. A neural group of centres in relation to the brain and nerve-cord.
2. A visceral group in relation to the alimentary tract, liver, and gonad.
3. A caudal group on the upper surface of the tail.

The accessory group comprises centres on the eye-stalk, in the antennæ, tail-fan, and brood-lamellæ of the female.

The neural group is segmentally arranged; a median or a pair of centres being placed opposite to each ganglion. The caudal group is median and segmental. The visceral group is in part median, in part paired, and its segmental character is hardly less clearly defined. The distribution of the individual components of each group is rigidly constant.

The further description of these groups may be easily followed by reference to Plate 21, figs. 13, 15, 18. The neural centres are related to the brain, nerve-cord, bases of the appendages and skin of the ventral surface. Thus, there is a pair over the brain; a pair at the bases of each of the antennæ and lateral to the connectives joining the brain and cord; a median centre between the first, and another between the second maxillæ, in both cases lying above but closely applied to the ganglia of these segments; then a pair at the sides of the cord opposite to the bases of the thoracic limits; lastly, in the abdomen, each segment has apparently two centres, one anterior and another (ganglionic in position) posterior. But each of the latter on a side view is clearly divided into two centres, one—the lower—resting on the ganglion, and the other—the upper—lying in the flexor muscles. In the last segment the muscular centre is constantly and specially related to the anal muscles.

The visceral group of centres is disposed as follows. On the upper surface of the stomach are two median centres. Under the elongated heart, two large and important centres are found; one beneath the gonad, close to the junction of the liver lobes, and the other immediately under the posterior border of the carapace. Both rest on the sheath of the gut and are therefore well below the epidermis. The anterior one is vertically above the third thoracic limb and lies between the upper ends of the pleuræ of this segment; the posterior one is similarly related to the sixth thoracic segment. The rest of the visceral group consists of centres above the intestine.

The caudal group consist of a median dorsal centre, dermal in position, on each of the abdominal segments and on the last thoracic segment.

If we omit for a moment the accessory group of centres on the ends of the body, the system formed by the neural, the visceral and the caudal groups presents certain well-defined features. It is centralised about the median plane and composed of a constant and largely segmental series of centres developed in relation to the central nervous system, the gut and the caudal surface.

The accessory group on the other hand shows a relation to outlying structures. On each of the eye-stalks an optic centre is constantly present behind the cornea. In the antennal scale five centres occur, one in the peduncle of the antennule and one at the base of the endopod. Each of the brood-lamellæ of the female, which are known to be the hypertrophied epimera of the last three thoracic legs, bears a row of chromatophore-centres; whilst on each of the uropods a single row, and on the telson a double row, of centres is developed.

Having regard to the peculiarities of the three chief groups of chromatophores both in *Macromysis flexuosa* and other crustacea which, as we shall see, possess these groups, we shall refer to them as the *primary system of chromatophores.*

B. *The Chromatophore-Branches.*

1. The branches of the neural group of chromatophore-centres supply, *i.e.*, run in relation with and invest, the central and peripheral nervous system, the muscles and skin of the tail, of the anus, of all the appendages, and the skin of the carapace; that is, all the superficial and deep organs of the main mass of the body, the alimentary tract and parts of the tail-surface alone excepted.

2. The branches of the visceral group supply the stomach, "liver," gonads, part of the carapace and the intestine.

3. The branches of the caudal group are confined to the skin and extensor muscles on the upper surface of the tail.

The branches of the accessory group supply the tissues in their immediate neighbourhood.

The branches as a whole possess well-marked characters. They are frequently of great length (2 millims. or even more). They subdivide into luxuriant ramifications which form investing sheaths to the deep organs and terminal arborisations in the skin. These characters are best developed in the branches of the neural group, which, in this as in other ways, is the dominant component of the chromatophore-system.

C. *The Chromatophore-Pigments.*

The majority of the centres contain (1) a large amount of a brown pigment largely insoluble in alcohol, but converted to a reddish tint and finally decolourised by oxidising agents such as chlorine, and (2) a smaller quantity of a substance bright yellow or white by reflected, but greyish by transmitted light. This substance so generally present in crustacea appears to have a crystalline form. Its chemistry, however, still awaits investigation.

The brown pigment occupies the greater part of the branch-system and gives rise, when fully expanded, to the black colour of *Macromysis flexuosa.* The yellow substance does not mix with the brown. It occupies a special series of branches and reacts to stimulation at a slower rate. On the stomach, liver and intestine it is well-developed, but is largely hidden from view by the paired fern-like expansions filled with this yellow substance which proceed from the caudal and neural centres. These expansions confer upon *Macromysis flexuosa* its characteristic colour-pattern. But underneath this superficial ground colour of brown relieved by yellow or white tracery, is a deeply placed system of branches on the gut, in the muscles and over the nerve-cord, that takes little or no part in the final colour-display.

D. *Histology of the Chromatophores of Macromysis flexuosa.*

(Plates 21, 22, figs. 19–23.)

The mature chromatophores are not single cells but are complex organs, the structure of which varies with their position in the body. In the telson and tail-lobes the centre of the organ (Plate 22, fig. 23, *Membr*) consists of a spherical thin-walled bag (·1–·2 millim. in diameter), pierced by a number of cells varying from five or six to eight or nine according to the age of the chromatophore. Each cell projects into the bag and is produced outwards into a branched fibrillated process. The nucleus is placed at the central end of the cell. The bag itself is formed by a flattened epithelium and contains the pigment in a clear or granular matrix.

On the brood-lamellæ (Plate 22, fig. 22) each chromatophore is composed of a large (often ·78–·75 millim. in diam.) lenticular centre and strongly developed branches. The central portion is apparently cytoplasmic, finely granular and slightly fibrillated. It is perfectly continuous with the branches. At the point where these commence or just beyond their point of origin, a small group of nuclei occurs. The protoplasm of the branches is markedly fibrillar both in fresh and preserved preparations. The centre of the chromatophore is bounded by a distinct membrane which appears to be continued round the branches.

The neural and caudal chromatophores exhibit a third type of structure. They consist of a large number of cells, fused at the centre with each other and with a protoplasmic mass in which a more refractive and densely staining body is often present. The body, however, is not a nucleus; it has no network, and is probably a product of the activity of the surrounding protoplasm. In these chromatophores the nuclei are more centrally placed than in the other two types, the branches are stouter and more numerous, and the centre attains a greater size and a greater capacity for producing and storing pigment.

In all types of chromatophore the branches of these organs, particularly of the neural group, attain a great length (2 millims. in extreme cases), and end in a definite terminal arborisation in the skin and viscera in a simpler manner on the nerve-cord and muscle.

Repeated experiments of stimulation on the same chromatophore cause it to contract to the same centre, and to expand into the same branches, and so produce the same pattern. These chromatophore-endings, however, are frequently so intricate as to give rise to the appearance of a plate of pigment, for example, on the eye-stalk and on the surface of the tail. In such cases it is difficult to determine whether the structure is the same as that just described for the main trunks, or whether the branches ultimately end in connection with a system of tubes.

Before leaving the histology of the chromatophores, we call attention to a glandular tissue with which they are intimately connected (Plate 22, figs. 22, 23). Each chromato-

phore-centre is surrounded by a zone of cells, with very large deeply-staining nuclei; and a strand of the same tissue runs from each chromatophore to the next. The chief development of this glandular epithelium is found at the posterior edge of each abdominal segment above and below, at which points it forms a broad band of squarish closely fitting cells, which appear to belong to the deeper layer of the epidermis. The visceral chromatophores, and those of the brood lamellæ (Plate 22, fig. 22), are also provided with a connecting band of the same curious tissue, which is, however, more lax and deeply placed. Many of the cells are pyriform, and they may unite together by their narrow ends. Their protoplasm presents different degrees of vacuolation and of granularity, indicating phases of secretory activity.

Close as is the relation of this glandular tissue to the centres of the chromatophores, its position towards their branches is yet equally intimate. But whether these cells have anything to do with the origin of chromatophores, or with the production of their pigments, is at present unknown.

E. *Development of the Chromatophores in Macromysis flexuosa* (Plate 21, figs. 19–21).

1. *The Centres.*—The earliest stage we have observed in the formation of this system occurs in embryos of 2 millims. in length, taken from the brood-pouch of the female. The neural group of centres was represented by the pair over the brain and at the bases of the antennæ. Later on, as the other appendages develop from before backwards, the other neural centres appear at their bases. In each segment of the abdomen only two centres, one anterior and one posterior, are present in the late embryo. The next group to appear is the caudal, which likewise develops from before backwards; and, last of all, the visceral. In late embryos the accessory group is represented by the optic centre, by two centres in the antennal scales, two in each of the tail-lobes (inner and outer), and by a pair in the telson. Before birth, therefore, all the centres of the three chief groups, and some of those of the accessory groups, are present in their definitive position.

We have followed the development of some of the neural centres (Plate 21, fig. 20). These organs arise as prolifierations of the epidermis, which sink into the deeper tissues. They are solid ingrowths which, at the earliest stage we have observed, are already composed of several cells surrounding a granular pigmented enucleate plasm. This group of cells separates from the surface. The cells grow out to form branches, which, however, remain unpigmented till a late stage in development. In the general conclusion that the chromatophores of *Macromysis* are products of the epidermis, we are able to confirm WAGNER (1896). WAGNER has already described this development for what he calls glands ("Pigment-drusen"), but he failed to recognise that these glands are the chromatophores.

The changes which subvene in the chromatophore-centres after the birth of *Macromysis* are but few, and comparatively unimportant. The only addition made

to the three chief groups, is the subdivision of the posterior centre in each abdominal segment into a dorsal, purely muscular centre and a ventral, mixed one. The additions to the accessory group consist of a few centres in the antennæ and tail-lobes, and, at the time of maturity, of centres in the brood-lamellæ.

2. *The Branches.*—The development of the branches is a much longer process; for, whereas the advanced embryo contains all the important centres of the adult, only the main chromatophore-branches are present at that stage. The luxuriant branching and definite terminal arborisations of the later stages are not even indicated, and, consequently, the colour pattern is not yet defined. It is only with the extension of the neural branches into the carapace and tail-terga, and the expansions of these branches into foliose terminations, that the pattern is gradually developed.

3. *The Pigments.*—In the early embryo only one substance is present in the neural centres. It is of an opaque dead black tone when seen in mass, but is dark brown in a finely divided state. In ripe embryos the neural centres are still without the yellow reflecting substance which is present in adult animals. The caudal centres are, from the first, filled with this yellow substance, to which the dark brown pigment is subsequently added.

F. *Summary.*

The chromatophore-system of *Macromysis flexuosa* consists of three main groups of centres. Of these groups, the neural is predominant. Its centres are the first to develop, appearing first on the brain, and later at the bases of the budding appendages. The caudal group develops after the neural, and the visceral after the caudal. These groups arise in the embryo, and persist with but very slight modification throughout life. The same is true of the accessory group of outlying chromatophores: that is, the chromatophore-system of the adult is fundamentally that of the embryo. The neural centres develop as thickenings of the epidermis. Groups of cells lose their connection with the surface, and come into close relation with the sheath of the nerve-ganglia. The chromatophore now consists of a number of cells surrounding a central cytoplasmic enucleate mass: that is, the chromatophore at this stage consists only of a centre in the sense in which we have frequently used that term. Branches grow out from the cells, ramify again and again, and ultimately terminate in definite arborisations. From the time of the earliest appearance of the branches, the pigments contained in the centre are functional, now flowing out into the branches, now contracting again to the centres. Thus the inconstancy of coloration of *Macromysis flexuosa* is an inconstancy of coloration only. The chromatophore-system and its contained pigments are constant, and the inconstancy is due to the ebb and flow of the latter.

SECTION III.

Comparison of the Chromatophore-system of other Mysidæ with that of Macromysis flexuosa.

(Plates 18–21 and Table I., p. 365.)

We have examined this system in species of the following genera :—*Macromysis*, *Schistomysis*, *Neomysis*, *Mysidopsis*, *Leptomysis*, *Macropsis*, *Gastrosaccus*, and *Siriella*. In order to delimit the chromatophore-centres, it is necessary to cause the pigment to flow completely away from the branches and to collect in the centres. This may be done by placing the animal in the dark, or under the influence of scattered white light. As this was not done by previous investigators, we are unable to utilise the incidental references to coloration that occur in the works of Sars (1876, 1879, and 'Crustacea Caspia,' 1893–5) and Norman (1892).

All these genera are characterised by the possession of a common centralised type of chromatophore-system, which we term the primary system. In some (*Macromysis*, *Schistomysis*, *Neomysis*, *Gastrosaccus*, and *Siriella*) the three constituent groups of chromatophores described in *Macromysis flexuosa* are fully represented. In others (*Leptomysis*, *Mysidopsis*) the caudal group is absent. The neural group persists in all.

The characters of the primary system are :—paucity in numbers of the component chromatophores, consequent on their segmental arrangement; centralised position of their centres; far spreading and luxuriant branches, the terminal arborisations of which form investing sheaths about the organs to which they run; and above all, persistence of the embryonic chromatophores as those of the adult.

Except *Schistomysis*, each of the genera, and the majority of the accepted species, severally exhibit a constant modification of this common plan, the details of which can be determined by reference to Table I., where also it will be seen that *Schistomysis* agrees with *Macromysis*. These modifications are due to the presence of paired or unpaired chromatophore-centres in particular segments; to the shape and extent of the terminal arborisations of the chromatophore-branches, and to the distribution of certain pigments within the centres and along the branches. For example, *Schistomysis arenosa*, *Sc. ornata*, and *Macromysis inermis* have almost the same number, and the same general arrangement of chromatophore-centres, but their branches and arborisations are so shaped and pigmented as to give each species a distinctive coloration.

The accessory group in these genera resembles that of the type *Macromysis flexuosa* in its position on terminal organs, the eyes, antennæ, tail-fan, and brood-lamellæ. In some genera the usual centres in the telson are replaced by a pair of centres at, or just in front of, its base, and ramifying within its substance. In

Macropsis, additional centres are found in the basal joints of the thoracic legs. The accessory group is to be regarded as arising from the neural group in connection with outlying, chiefly nervous structures, and, as such, is part of the primary system. But, in as much as the process of development of the chromatophore-system in higher Crustacea (Decapods) is one of decentralisation—resulting in a secondary system, this accessory group, which already reveals a commencement in the process of decentralisation, may be considered as an incipient secondary system.

The structure of the chromatophores in these genera is similar to that described in Section II., p. 304. In all cases that we have examined these organs consist of several cells. The thickened central ends of these cells either fuse with a central cytoplasmic body, or project into a central cavity, in either case being bounded by a membrane. The tapering outer ends of these cells run outwards, and terminate in excessively fine tubules, or in plate-like arborisations. The contained pigments and reflecting substances are limited to the dark brown granular pigment (most *Macromysis, Schistomysis, Mysidopsis, Leptomysis, Macropsis*), or a red pigment (*Macromysis inermis, Siriella*); the reflecting substance is usually yellow, but blue and bluish-green occur in addition (Plate 20, figs. 8, 9). No yellow absorbent pigment and no blue pigment appear in the chromatophores, though in *Macromysis* a blue substance appears at nightfall in the blood, and in the neighbourhood of the muscular processes of the chromatophores.

We conclude that the littoral and sub-littoral genera of Mysidæ which we have examined and recorded possess a primary and an incipient secondary system of chromatophores essentially similar to those described in the type *Macromysis flexuosa.*

There are, however, a number of deep-sea genera in which the primary system is apparently reduced, and the secondary system greatly developed. From SARS' monographs (1879, 1876) on Norwegian and Mediterranean Mysidæ, it appears that *Mysideis, Mysidella Amblyops,* as well as the *Erythrops*-group (typically, but not exclusively deep-water forms) possess small, scattered, superficial chromatophores. The importance of determining the nature of this diffused arrangement will become clear when the next section has been read. For, in that section, we describe the dominant part played by the scattered secondary chromatophore-system of Decapod Crustacea. The chromatophores of deep-sea Mysidæ, as of littoral forms, have, however, only been incidentally noticed by investigators. Until their structure and arrangement have been ascertained, and until we know whether they respond directly or indirectly through the eye to light, a discussion of the relation of this scattered system with that of Decapods could not be profitably undertaken.

SECTION IV.

THE CHROMATOPHORE-SYSTEMS OF DECAPOD CRUSTACEA; THEIR NATURE AND DEVELOPMENT.

(Plates 22 and 23, Table II.)

A. *Introduction.*

Owing to the supposed inconstancy and systematic unimportance of the chromatophores, the literature of Decapod development contains no complete description of the origin of these organs. EHRENBAUM'S work on the shrimp (1890) and SARS' work on the Crangonidæ (1890) are the least incomplete in this respect. Even in these cases, however, the references to chromatophores are quite inadequate, and we are compelled to describe the arrangement of these organs fully without further reference to previous work.

In the following section we trace the development of the chromatophore-system and colour-patterns in Decapod Crustacea of the genera *Crangon, Palæmon, Hippolyte, Galathea, Carcinus* and *Portunus.* The general features of this chromatophore-system and of its development will first be described, afterwards the manner in which, in each species its component chromatophores unite to form this system, and, lastly, a comparison and a contrast will be drawn between this Decapod system and the Mysidean system that we have already described.

In tracing the development of the chromatophore-system in these shrimps, prawns and crabs, we have had to content ourselves largely by piecing together the evidence of newly hatched larvæ, of later larval stages obtained by the tow-net, and of adolescent stages when the animals have taken to the sea-bottom or sea-weed. The difficulties in the way of rearing these Crustacea from the egg to the adult have so far proved insurmountable. We hope, however, to overcome these difficulties in subsequent trials. Even in the present instance we have been able to rear the shrimp through several changes, and the prawn (*Palæmon*) through the "stalked-eye" stage, and have thus been able to confirm the evidence obtained from specimens taken at large.

B. *General Character of the Chromatophore-system of Decapods.*

The general characters of the chromatophore-system of the Decapod Crustacea which we record, are: The large number and the scattered, irregular arrangement of the chromatophores; the limited reach and paucity of their branches; the decentralisation of the system as a whole.

The pigments contained in this system are optically of two kinds—absorbing and reflecting. The former remain of the same hue when viewed either by

transmitted or reflected light, and are merely lighter or darker in tone. Of such absorbing pigments, red, yellow, brown and violet and diffuse blue are present. The latter—the reflecting substances—are only effective when viewed by reflective light, when they appear white, yellow, greenish or blue as the case may be. Several pigments may occur in the centre of a single chromatophore, and the evidence goes to show that each pigment occupies one or more "cells" and processes of these cells, and that the chromatophores are clusters of such. Furthermore, the branches of adjacent chromatophores frequently fuse, suggesting that they have budded off from a common origin. The chromatophore in the tail-muscles of *Hippolyte* and *Palæmon* often exhibit this appearance very plainly. In other specimens of these prawns and in crabs the individuality of the chromatophore-centres becomes lost: a sheet or column of diffuse pigment is produced, which defies analysis into separate chromatophores; but in which, nevertheless, governing centres of pigmentary attraction and pigmentary repulsion still exist. For at nightfall these diffuse inert-looking masses of pigment are converted into a number of isolated dots, the spaces between which are filled with a blue pigment. At daybreak the blue pigment disappears, and its place is taken by a sheet or column of dark pigment.

We are thus led to regard the scattered chromatophores of Decapod Crustacea as part of a system and not as so many isolated amœboid "cells." This system is developed superficially and also in relation to deep organs, particularly the muscles. Its superficial part when filled with pigment is effective as colour. Its deep part is either ineffective, being hidden by that of the surface, or has too little pigment to make an impression on the eye, or, again, it may serve as a background against which the reflecting substance may be clearly seen.

C. *The Development of the Primary and Secondary Chromatophore-systems in certain Decapod Crustacea.*

1. The shrimp (*Crangon vulgaris*) (Plate 23, figs. 35–40), acquires a series of chromatophores while within the egg-membranes. These centres form two groups, neural and caudal. The neural group develops as in *Mysis* from before backwards; but, owing to the suppression of the majority of thoracic segments and appendages in the early stage, few of the neural centres in the thorax are represented in the embryo or zoea.

At the time of hatching, the zoea possesses neural, caudal and accessory groups of chromatophore-centres. The neural group is arranged at intervals along the nerve-cord and at the bases of certain appendages. The caudal group is confined to the upper surface and sides of the tail. There is as yet no visceral group. The accessory group consists of three centres in the antennule, a pair on the carapace, and at the point of junction of exopod and endopod in both the second and third maxillipede.

The branches of the neural centres supply the nerve-masses of the head and thorax

and tail, the appendages, the labrum and the flexor muscles. From the centre at the base of the second maxilla, an additional long branch is given off to the carapace. The branches of the caudal centres supply the skin of the tail.

Each centre and its branches are filled with two substances—a claret-coloured pigment and a yellow reflecting substance. Even before birth, the chromatophores exhibit the phenomenon of ebb and flow of pigment and reflecting substance. But there is no gross colour-effect, even when the branches are filled with these substances.

We wish to draw attention to certain remarkable features of the chromatophore-system just described, in the pelagic zoea of the shrimp. As in *Macromysis*, this system is composed of neural, caudal, visceral and accessory groups of centres. The individual members of each group can, in most cases, be safely homologised with particular centres in *Macromysis flexuosa* or *M. inermis*, the only conspicuous exceptions being the pair of centres on the labrum, the centres on the carapace and in the maxillipedes. The branches have a similar spreading character, and in the second maxilla run upwards to supply the carapace exactly as in *Macromysis*. They supply exactly parallel organs in the two cases. The pigments are similar in character, both an absorbent and a reflecting substance occurring in each centre in both shrimp-larva and *Macromysis*. In short, the chromatophore-system of this zoea is built on the same plan as that of Mysidæ. It is perfectly constant, and possesses the Mysidean characteristics of grouping, centralisation and paucity of numbers. We may, therefore, speak of the median and admedian, neural, caudal and visceral centres as the commencing primary system, and the accessory group as the commencing secondary system (see Plate 23, figs. 36, 37).

The further development of these two systems requires separate consideration. The primary system of the zoea is slowly increased during the *Mysis*-stage by the addition (1) of centres added to the neural group; (2) of visceral centres. As the thoracic limbs appear, new chromatophores develop at the bases of the fourth and sixth limbs. At the same time, the visceral group receives accessions from the development of a pre- and post-cardiac centre, comparable to those found in *Macromysis*. By this time, the shrimp has reached the "*Mysis*-stage," the grade of development when all the thoracic limbs are present, and when most of them have their temporary exopods. At this stage the primary chromatophore-system is still more closely comparable with that of *Macromysis*, *e.g.*, *M. inermis*, than it was in the zoea, and this primary mysidean system persists. The shrimp retains throughout life the primary chromatophore-system developed in the egg. The masses of pigment which, in the adult, occur round the ganglia of the abdomen, at the bases of the majority of thoracic limbs, and of the mouth part, are simply the persistent enlarged centres of the neural group. The remaining part of the primary system—the visceral and caudial groups—also persist, but are obscured by the luxuriant growth of the secondary system, which we must now describe.

In the zoea, this system was limited to a few centres in the antennules, maxillipedes and carapace. Few as they are, their position indicates that these chromatophores are not represented in *Macromysis*, for it is characteristic of the Mysidæ we describe, that the appendages and carapace have no chromatophores, but are supplied by pigment from the branches of the neural centres. In the *Mysis*-stage of the shrimp, many additional secondary centres have arisen, one on each abdominal pleuron, a second pair on the carapace, and several in the joints of the new thoracic limbs. As the adolescent stage is reached, a transverse row of superficial centres is established across the upper surface of each tail-segment, others in the telson and uropods, and a double longitudinal row now runs along the carapace. In still later stages, the whole of the upper surface becomes thickly sown with chromatophores, to the pigmented branches of which the definitive speckled colour-pattern is due. By suitable stimulation, this pigment may be caused to retract, and then the persistent caudal and visceral centres can be identified by their relation to the middle line of the tail-segment and to the heart. (Plate 23, fig. 40.)

The development of the chromatophore-system in the shrimp is therefore as follows. In the embryo, a centralised system of caudal and neural groups is established on the upper and lower surfaces of the body, and a scattered secondary system is begun in the antennules, carapace and limbs. In the *Mysis*-stage the centralised system is fully developed and is clearly comparable with the primary system of a *Macromysis*; the secondary system has increased but slightly, and is only partially of Mysidean type. At the close of larval life, this latter, scattered and decentralised system rapidly develops, new centres being added in the skin of the upper surface, whilst on the under surface the neural group is still dominant. Finally, the secondary system completely overlays the primary one on the dorsal surface, and establishes the grey coloration of the adult. The figures 36–40 on Plate 23 illustrate this description.

We may conclude this section by a short description of the changes in the pigments and the coloration of the animal. The chromatophores of the zoea contain as we have said both a claret-coloured pigment and a yellow reflecting substance; but even in the *Mysis*-stage, the centres are not sufficiently numerous and close together nor are their branches so finely sub-divided as to give rise to anything more than a general greyish tint when viewed as a whole. In adolescent shrimps, however, the claret-colour has been replaced by a violet tint and, in some chromatophores, a red pigment (orange-coloured when seen in the branches) has arisen. Thus, in the adult, the chromatophores may contain violet pigment, or violet pigment and yellow reflecting substance, or a red pigment may also be present. These substances have been already correctly recorded by POUCHET, who discovered that they behave differentially with regard to a given stimulus. The shrimp, however, makes little use of its opportunities. Notwithstanding the great potentialities for coloration that lie in the possession of three differently coloured substances, each of which is

somewhat different in tone when seen in mass from what it appears when expanded into fine branches, the colour of the shrimp merely oscillates between speckled grey of a lighter or darker shade and a transparent almost colourless tint.

2. *Crangon fasciatus.*—The banded shrimp possesses, in its zoea-stage, a chromatophore-system closely resembling that of the larval common shrimp in general features, but exhibits slight though constant differences of detail. The most important of these are (1) the presence of a pre-cardiac elaborately branched element of the visceral system which in the common shrimp develops very late and remains small; (2) the violet colour of the pigment which is only attained in the later stages of *Crangon vulgaris*; (3) the presence, in the *Mysis*-stage, of paired neural centres opposite the bases of each pair of thoracic limbs; (4) the very late appearance of a secondary system of chromatophores. In almost all these points, *Crangon fasciatus* agrees even more closely with the Mysidæ than does its more abundant ally. The differences are also of interest as showing how constant is the arrangement of the centres, the distribution of the branches, and the colour and colour-changes of the pigments, in each species. We have not been able to follow the development of the chromatophore-system beyond the *Mysis*-stage in *C. fasciatus*, but the foregoing account serves to show that a primary system is developed, even more closely Mysidean in the number and arrangement of its members than is the system of *C. vulgaris*. In the adult this system is concealed, as in the latter species, by superficial scattered chromatophores, which are so abundantly developed and pigmented at intervals as to give rise to that banded pattern, and brown, white, and black colouring distinctive of *Crangon fasciatus*.

3. *Hippolyte varians.* (Plate 23, figs. 41–50, and Plate 22, fig. 23A.)—The main features of the development of the chromatophore-system in this species are similar to those in the shrimp. The zoea, at the time of hatching, possesses neural and caudal groups of centres, traces of a visceral group, and of a small accessory group. The branches are well developed and the ebb and flow of pigment and reflecting substance is, even before birth, a striking phenomenon. The only general colour-effect is a grey-green tint visible when the zoea is examined in the expanded phase against a black background. As in the shrimp, the number and arrangement of centres and their pigments are absolutely constant.

In the zoea, the neural group includes some centres not found in the shrimp till a late stage in development; and it is necessary to describe the groups of chromatophores both on this account and also because the number and arrangement of their constituent members is constantly, if slightly, different in different "species" of *Hippolyte*. In *H. varians* the neural group contains four paired centres at the bases of the two antennæ, a median centre on the inferior, and a pair on the upper surface of the brain, another in the labrum, a large median centre above the lower lip, a pair at the base of the first maxillipedes and a centre below the anus. The visceral group is indicated merely by a pair of centres at the junction of the liver-lobes. The

caudal centres are in part median (on the first three tail-segments), in part paired (on the third and fifth). The accessory group comprises a pair of centres in the distal joint of the antennules, in the proximal joints of the second and third maxillipedes, and a pair on the hinder border of the carapace. (Plate 23, figs. 42, 43.)

From this description aided by a consideration of figs. 41–43, it will be clear that the zoea of *Hippolyte varians* possesses a partial neural group (the abdominal centres seen in the *Crangon*-zoea being absent at this stage), a partial visceral group, and a fairly well-developed caudal group. In short, there are at this stage the commencing primary and secondary systems of chromatophores, many of the members of which are homologous with those of *Crangon* and of *Macromysis*.

The next stage referable with certainty to *Hippolyte varians*, that we have been able to obtain, is not the *Mysis*-stage, but the adolescent one when the animal has just abandoned its pelagic larval life, and adopted the sedentary weed-haunting habit of the adult. The chromatophore-system is no longer perfectly uniform and constant as in the larva. But notwithstanding these variations, the significance of which we discuss in Section V., the following changes in the development of the primary and secondary systems can be recognised in almost all adolescent *Hippolyte varians* of 3–4 millims. length. The neural group is now almost complete. It is composed of the persistent larval centres on the brain, near the bases of the antennæ, labrum, maxillæ, and maxillipedes; and, in addition, new centres have been added between the bases of the newly developed thoracic legs and on each of the abdominal ganglia. The resemblance of this neural group to the ventral chromatophores of *Macromysis* is now a much closer one than was the case in the larva. In the visceral group, a gastric centre, and a pre- and post-cardiac centre, a second pair of hepatic centres and a small number of intestinal ones have been added to the hepatic visceral centres of the larva, so that this group corresponds very closely indeed with the visceral chromatophores of *Macromysis*. The caudal group has become altered in a manner which brings it into line, for example, with *Macromysis inermis*; for in each chromatophore the reflecting substance has separated from and lies behind the absorbent pigment. In the third segment of the tail the lateral centres have increased in size, and in the fourth, a median and a paired centre have arisen. Thus the primary system of adolescent *Hippolyte* is fully established, and corresponds with that of *Macromysis* in its grouping, centralisation and paucity of numbers. (Plate 23, figs. 50, 51.)

In these changes, all or nearly all early adolescent specimens agree, however different may be their general colour or pattern. The differences are due to variations in the secondary system of chromatophores. In the zoea of *Hippolyte*, this system was constant, and confined to the antennules, maxillipedes, and carapace, where, however, it was so feebly developed as to produce no distinct colour or pattern. In the early adolescent stage, it has gained in numbers, extent of branching, and impressiveness, but shows only an indication of its future importance. In as far as the general coloration of these early adolescent *Hippolyte* is uniform, it

is so from a largely uniform primary system, and a secondary system, which begins at certain points, and at these only. In as far as the coloration is distinctive, it is so from a special development of the hitherto uniform secondary system along special lines. We may distinguish the uniform beginnings of the secondary system and its special developments in *Hippolyte* in the following way: this system, begun in the larva, increases in the majority of early adolescent *Hippolyte* by proliferation in (*a*) the third segment of the tail, (*b*) in the basal joints of the limbs and in relation to the gills, (*c*) in the antennæ and tail-lobes. Its special developments take place (*a*) in the flexors and extensors of the tail, (*b*) in the neighbourhood of the liver, (*c*) on the carapace and surface of the tail-segments. When all these regions are thickly sown with small chromatophores, a uniform coloration, a "monochrome," is the result. When one or more of these are the seat of active formation of chromatophores spots, bars and lines are the result; "barred" and "lined" colour-forms are produced. Hypertrophy of superficial scattered chromatophores may produce a pseudo-monochromatic effect, concealing underlying segregations of centres into bars and stripes; or the spots and bars may fuse and form a monochrome. In whatever fashion the coloration of *Hippolyte varians* occurs, it is due to the secondary system, which hides a persistent primary system. On the ventral surface, the neural group of this primary system is usually dominant. Thus there is in *Hippolyte varians* (Plate 23, figs. 41–50):—

A. A primary system of chromatophores, begun in the embryo, completed in early adolescent life, and persisting in adult life.

B. A secondary system, begun in the embryo, enlarged at first uniformly along certain lines in the early adolescent stage, then diverging in different individual *Hippolyte* along special lines. This system increases throughout life.

C. The primary system has little or no share in determining the colour or colour-pattern. It is usually dominant on the under surface, where, however, it is naturally concealed.

D. The secondary system develops in part in relation to the primary one (*e.g.*, muscle-centres formed under caudal primary centres, liver-centres in relation to visceral chromatophores), in part independently (carapace, sides of tail). It is effective, from the early adolescent stage onwards, in producing the colour-impression.

4. *Hippolyte cranchii.*—The development of the chromatophore-system in this species is essentially similar in its general features to that of the preceding one, but with certain constant differences which illustrate the taxonomic value of this system. The zoeal system is, save for the presence of an additional visceral centre, in front of and below the heart (the pre-cardiac centre of *Macromysis*), identical with that of *H. varians.* In the adolescent stage the similarity is maintained.

The primary system is developed in a manner parallel to that of *H. varians.* A special "lined" adolescent coloration is developed in connection with this primary system. The secondary system occurs in the muscles, carapace, the hepatic region,

limbs and tail. In this species, however, the adult coloration is constant, or almost so, and is due to bands of superficial chromatophores containing much reflecting substance across the head, thorax, and tail. Underneath these bands, which occur as an occasional coloration in *H. varians*, the adolescent secondary system persists, and if both of these systems be contracted by subjecting the animal to scattered white light, or to prolonged darkness, the primary centres with their characteristic groupings are revealed. We may say, therefore, that the peculiarities of this species are its more constant adult coloration, and its simpler colour-history. It agrees, however, with certain varieties of its protean ally *H. varians* in the general features of its larval, adolescent, and adult development, and may be said to represent a special case of *H. varians*. This constancy of coloration in the adult is probably associated with the habits of *H. cranchii*. Unlike *H. varians*, it is rare amongst weeds, but is abundant at low tide-mark under stones, especially where the sand or other substratum contains much water.

5. *Hippolyte gaimardii*.—This species, which we have received from the Millport Biological Station, has the aspect and coloration of a *Pandalus*. The body is covered with minute chromatophores arranged, as in a prawn, in lines down the segments, but without any bold pattern. We have been able to determine that the primary system persists in neural, visceral, and caudal positions, and that this system arises in the embryo in a manner closely similar to that of either of the foregoing species, but with certain constant differences of detail, the chief of which are:—the almost complete development of the caudal group; the presence of a pair of posterior hepatic centres; and the absence of a pre-cardiac centre in the visceral group.

The extraordinary agreement between the adult coloration of this *Hippolyte* and that of certain *Pandalus* is due to a great superficial, as well as to muscular and visceral proliferation, of secondary scattered chromatophores. It would seem as if similar surroundings had produced a similar modification of the secondary system. But, as we describe below, the true prawns hasten the development of this system, so that it is strongly developed even in their zoea stage; whereas, in *Hippolyte gaimardii* the zoea only possesses the centres in the carapace, antennules, and maxillipedes, that we have described for the larva of *H. varians*.

6, 7. *Palæmon squilla*, *P. serratus*. (Plate 22, figs. 29–34, and Table II.)

The adult coloration of these prawns is constant, and mainly due to masses of superficial discrete chromatophores; though in the muscles, and taking but little part in the general colour-effect, is a system of intercommunicating pigmentary branches. On the ventral surface the ganglia of the abdomen are clearly indicated by masses of pigment—the abdominal neural group—and between the joints of the thoracic limbs, and at the bases of the mouth parts and antennæ, other persistent chromatophores of the neural system can be detected.

The development of the secondary chromatophore-system reaches an advanced

stage before birth. The zoea of *P. squilla* possess four pairs of scattered but constant, small centres on the liver, three pairs on the carapace, a pair of small, lateral centres on the pleura of each of the first three abdominal segments, and in the basal joint of the three maxillipedes. The zoea of *P. serratus* has even more centres on the carapace, whilst on each segment of the abdomen a pair of pleural centres is present, even before birth.

As regards the primary system, the two species agree very closely. The zoea of each species possesses certain elements of the neural, caudal, and visceral groups: two pairs of antennary, two pairs of maxillary, and pre- and post-cerebral centres, and an anal centre from the neural group; three chromatophores on the third tail segments represent the caudal, and a pair of hepatic centres the visceral group. The later development of this system has not been followed in detail, but the adult prawn preserves its primary system as fully as does *Crangon* or *Hippolyte*, though it is completely overgrown on the upper surface by the extensive secondary system.

The salient feature of the primary system is the extraordinary length, and the upward curve of the branches of the two maxillary and antennary centres. In *Macromysis*, the branches of these identical centres supply not only the organs in their immediate neighbourhood, but also send long branches to the carapace. In the zoea of *Palæmon*, as is shown in figs. 29 and 30, the branches of the maxillary centres are very numerous, and spread upwards in such a fine meshwork as to give the optic ganglia the appearance of a yellow patch, whilst the antennary centres send branches upwards to the carapace.

The distinguishing feature of the secondary system is its comparatively high degree of development even before birth. Each of the centres on the carapace and pleura marks the commencement of one of the oblique lines of pigment that characterises the coloration of the adult, whilst the numerous scattered centres over the liver of the zoea give rise to that mass of brilliantly coloured chromatophores over the stomach of the adult (Plate 22, figs. 33–34). Thus these two species of *Palæmon* are distinguished by a hastening of the development of the secondary system, the elements of which mark out the characteristic coloration of the adult.

8. *Brachyura.*—The shore-crab, *Carcinus mœnas* (Plate 22, figs. 24–28). In all the forms we have so far considered, the cuticle is transparent and allows the subjacent pigments to show through its substance. In the adult crab the opacity of the cuticle precludes the possibility of distinguishing anything more than a marbling of colour due to pigment in the "shell" itself. Under this carapace and closely attached to it is a thin layer of chromatophoric pigment developed in or under the epidermis. The individual chromatophores are as a rule not distinguishable, but their centres are indicated by minute red dots, and their branches by a mesh-work of red pigment and yellowish reflecting substance; a diffused blue pigment is also frequently present. We have not determined whether this apparently inert mass of pigmentary substances has in the adult crab lost all power of responding to light and other agencies by the

usual mode of flow of pigment. Such changes, if they do occur, could only be detected by removing pieces of the carapace. But in the earlier stages of growth, *e.g.*, in young crabs ¼ inch across the carapace, chromatophoric movement is still possible, and can be recognised owing to the comparative tenuity of the carapace. In the adult, however, the chromatophoric system is only effective in producing the pigment from which the carapace itself receives its supply. Its power of producing a colour-pattern directly has vanished: and, on the tail, the chromatophores themselves have, especially on the ventral surface, very largely disappeared.

It is therefore interesting to find (see figs. 24–28) that in the zoea and through the larval and post-larval (*megalopa*) stages, the shore-crab possesses a primary and a secondary chromatophore system of a very clearly defined character. In particular, the primary system is well developed and exhibits not only a general agreement with that of the Macrura but with that of *Mysis* itself; whilst the secondary system is retarded and in a late *megalopa*-stage is not more advanced than in *Palæmon* at the time of hatching. Even in the *megalopa*, the primary system of the crab is still dominant, and the superficial covering of secondary pigment which eventually grows over and hides it is only developed after the crab has passed through this stage and adopted the habit of the adult.

The primary system which, with little alteration, persists from birth to the end of and even beyond, the *megalopa*-stage, is composed of neural and visceral group, but the caudal group is entirely absent. The neural group is composed of centres over the brain, at the bases of the antennæ, in the labrum, at the base of the mandibles, of the first maxillæ, of the second and third maxillipedes, as well as a pair in each abdominal segment. This paired character of the neural group in the tail-region is not found in other crustacea we describe. Another noteworthy feature of these abdominal centres is their subdivision into a dorsal portion and a ventral larger moiety, the former supplying the place of the caudal group. The visceral group is, chromatophore for chromatophore, as far as it goes, identical with *Macromysis*. Thus we find a median gastric centre, pre- and post-cardiac centres. The primary system of the crab-*zoea* and crab-*megalopa* agrees in its grouping, centralisation and paucity of numbers with that of *Mysis*. The reduction of neural group in the thoracic region (at least up to the *megalopa*-stage, beyond which we have not followed it) and the absence of a caudal group are the only important points in which the primary system differs from *Mysis*, and even the latter negative character occurs in certain Mysidæ, *e.g.*, *Leptomysis*. (Plate 22, figs. 24–28.)

The secondary system of the zoea consists merely of two longitudinal bands of pigment on each side of the carapace, one over the mandible and the other over the maxillipedes, and of a centre in each of the two maxillipedes. There is also a paired centre in the optic ganglia and at the anterior and inner angle of the retina. In the early *megalopa* the longitudinal bands break up into separate chromatophores, and new centres are formed in the basal and distal joints of the newly developed thoracic

limbs. Later still, new centres are formed round the heart; but up to the latest *megalopa*-stage we have examined, there is no concealment of the primary system. Looked at from above, the visceral group is still distinct; from below, the neural group is well marked. In attaining the adult condition, the tail and its contained organs degenerate and concomitantly with the fusion of the abdominal ganglia with those of the thorax, the paired neural chromatophore-centres lose their individuality. The secondary system spreads superficially over the skin of the carapace and limbs and, together with the remains of the primary system, becomes reduced to a sheet of inert masses of pigment. Thus the last stage of chromatophoric evolution is attained.

The colouring matters of the crab-zoea are, like those of *Macromysis flexuosa*, a brown pigment and a yellow reflecting substance. In the *megalopa*-stage each chromatophore has increased in size and richness of branching, and contains a much larger quantity of both pigment and reflecting substance. As the large secondary centres in the carapace break up into several components, their pigment alters from brown to red; a change which is paralleled in *Macromysis inermis*, in which the chromatophores before birth contain a dark-brown substance, but as the branches develop the pigment which fills them appears of a red colour. It is only in older crabs that the blue substance is superadded to the others.

9. *Portunus pusillus*, *P. depurator*.—We have examined the zoeæ of these swimming crabs, and we find that their chromatophore-system agrees closely with that of *Carcinus*, though in some respects it is even less modified from the Mysidean type. This is clearly shown by the unpaired character of the neural centres in the abdomen and by the absence of large carapace-centres. The grouping of the chromatophores is characteristic. The neural group has the usual centres above and below the brain, at the base of the antennæ, in the labrum and mandible, a very large richly branched centre between the first maxillæ, one in each segment of the tail and an anal centre. The visceral group is composed of a gastric, a sub-cardiac, and a post-cardiac series. The caudal group is absent.

The pigments differ slightly from those of *Carcinus*. Each centre contains a granular substance, black in mass but claret-coloured when extruded, as well as a yellow reflecting substance.

10. *Galathea squamifera*.—The zoea of this, and of another undetermined, species of the genus possess a chromatophore-system which, while exhibiting a general agreement with that of other larval Decapods, shows certain peculiarities of grouping and pigmentation that give *Galathea*-larvæ a position intermediate between the Macrura and the Brachyura we describe.

The primary system is composed, as in crabs, of only two groups, neural and visceral. The secondary system is reduced to a pair of antennulary and to two pairs of maxillipedal centres. The neural group is represented by the anal centre as in *Hippolyte* or *Palæmon*; and as in *Hippolyte* and in crabs, possesses a specially large and sensitive median maxillary centre. The visceral centres are gastric and post-cardiac as in the crab.

The most distinctive feature of the chromatophores of *Galathea* is the immobility of their bright vermilion pigment. Except on the maxillary centre the yellow reflecting substance is absent.

D. *Summary.*

The chromatophore-systems and consequently the colour patterns of Decapods offer a sharp contrast with those of the Mysidæ. In the Mysidæ, the primary system is responsible for the colour of the animal; the secondary system, comprising the group accessory to the three main groups, is incipient and all but functionless. In the Decapods, the adult colour-pattern is the product of a secondary system of chromatophores which has come to overlie and obscure the primary system. The differences between the chromatophores of the two systems are not less well marked. Those of the primary system are profusely branched, few in numbers, segmentally arranged and centralised. Those of the secondary system are sparsely branched, numerous, irregularly arranged and decentralised. Nevertheless the chromatophore-system of the larval Decapod is more closely akin to that of the Mysidæ than to that of the adult Decapod. A *Mysis*-stage occurs in the development. In this stage, the primary system is represented by neural, caudal, and visceral groups of centres. The component chromatophores have the same characters in the primary system of Decapods as in that of Mysidæ. The very pigments of the chromatophores are the same in either group.

Up to the end of the *Mysis*-stage, the primary system dominates, holding as it were in check the incipient secondary system. After the *Mysis*-stage is passed, the secondary system gains more and more on the primary. To the latter, no new centres, to the former, a constant succession of new centres are added. Of these new centres some, though but few, arise in connection with the primary system, but most independently of it. They and they alone form now the working system, that is the system to whose pigment and pigment-distribution the colour and pattern of the adult animal are due.

SECTION V.

The Inheritance and Acquirement of the Chromatophore-systems and Colour-patterns.

It is evident from the foregoing section that the morphology of the chromatophores—the pigment-morphology of Crustacea—is neither so simple nor so meaningless as has been hitherto supposed. The existence in Decapod Crustacea of a whole system, the primary system of chromatophores, buried amid a dense overgrowth of superficial and deep scattered secondary chromatophores, shows that the chromatophores do not serve merely to produce a colour-effect. The orderliness of the steps by which the primary, and then the secondary, systems are established, shows that

their constituent chromatophores are not mere isolated cells of the skin or connective tissues ; the meaning of the systems is clearly a deeper one.

We have to remember that colour in the Mysidæ is chiefly the expression of the more superficial parts of the primary system, and in Decapods is mainly determined by the surface chromatophores of the secondary system.

The problem of colour inheritance and colour-acquirement is, therefore, part of the larger problem; is the form and coloration of the primary system of Mysidæ inherited or acquired, and is the same true of the persistent primary and the effective secondary systems of Decapods? In dealing with the special problem of constancy or variability of colour in the adult and growth-stage of any one form we have to ask, in constantly coloured forms, are the steps in colour-development directly preparatory to the final colour-display, or are there one or more special adolescent colorations? Lastly, in variably coloured adults we have to inquire whether the larval coloration is constant or variable, whether the colour-varieties are colour-races which breed true; whether the adolescent colorations are stages through which the animal passes on its way to a definitive colour-pattern; or whether the coloration varies with the environment, and ultimately is determined by it? To these questions carcinological literature affords no answer.

The problem of how far form and pigmentation of the primary and secondary systems of chromatophores in Crustacea are determined by inheritance, or by environment acting on hereditary structures, differs in an important manner from the problem of inheritance or acquirement of colour as generally stated. In the case of colours of eyes, hair, feathers, and other appendages of the skin, the form of the colour-elements, individually and collectively, has not hitherto been considered, whilst, in the case of individually variable animals, the constancy of form of the colour-system, as opposed to momentary or rhythmic ebb and flow of pigment, has been insufficiently realised, or not at all. We may, therefore, hope that, if we are able to reach any sound conclusions on the transmission and acquirement of the form and coloration of the chromatophore-systems of Crustacea, they will be found applicable to other cases, such as fishes and certain Mollusca, in which chromatophores play an important part in determining the colour of the animal.

A. *Mysidæ.*—We have shown that, in Mysidæ, the primary system is dominant; that each group of the system—neural, visceral, and caudal—is represented by a definite number of centres arranged in a particular fashion; that the neural group develops first, is the most constant, and, by its numerous far-reaching branches, supplies the greater part of the body with pigment; that the chromatophore-centres, the outlines of their branches, and their characteristic pigments, are present at, and even before the time of hatching. It is, therefore, highly probable that not only the form of the entire system, but of its centres and branches, and the colour of their pigments, are inherited. So true do Mysidæ breed, that some species, *e.g.*, *M. flexuosa* —perhaps the most abundant of all Mysidæ, and therefore exposed to great varieties

of environment—can be recognised when they have but two or three pairs of appendages, and are in an extremely early developmental condition. The same conclusion is true of the secondary system of these Schizopods. The retinal chromatophore, for example, whose branches form a plate of pigment over the optic ganglia, occurs in all the Mysidæ, and develops before birth. The centres in the tail-lobes and antennæ are present in the embryo, and either remain unaltered or multiply but slowly. It is, of course, desirable to test experimentally whether the development of the two systems is effected in its general form, or in detailed arrangement of its constituents, or in the colour of their pigments, by exposure of the female to different surroundings, and by exposure of the young after birth to varied conditions. In so far as some of the common Mysidæ do live or have been kept, some under dark surroundings and others under scattered light, the experiment has been made, and the result shows that the general form of the primary system, and the arrangement of its groups and their pigment, is not affected thereby. We conclude that, in the Mysidæ, the number and arrangement of the groups which make up the primary chromatophoric system, the pigments which they contain, and the resulting pattern, are largely, if not entirely, as much an inheritance as the development of the appendages.

B. *Decapods.*—In this group, the secondary chromatophore-system assumes such an extent of surface as to define the form and hue of the coloration, to which the primary system, as we have shown, contributes very little. The early rise of this primary system, however: its completion in the *Mysis*-stage: and its persistence in an unaltered, or but slightly altered, form throughout life, suggest that its main features are probably inherited. Whatever may be the use of this primary system, whether it serves now but as a stimulus necessary for the development of the secondary system, or whether it exercises some metabolic influence, such as many persistent rudimentary organs are known to do, it cannot be said to survive in virtue of being of direct use in contributing to the coloration of the body. Even if it be proved to give rise to some part of the secondary system by budding, yet the major part of this effective colour-system arises *de novo*, and in the shrimp, for example, appears to be absolutely independent of the primary system. Therefore, even if, as seems probable, the primary system is inherited, the derivation of the secondary system remains unexplained, and with it the problem of the inheritance of colour.

Crangon.—The problem here may be defined by examples. The shrimp develops the beginnings of its secondary system in the embryo, but only as a later but still pelagic larva is the system recognisable in its main outlines. On settling down on sand, the adolescent animal pursues the straight and direct course of development which leads to a grey, speckled coloration. The environment of the late larva and adolescent shrimp are widely different, yet the first prepares directly for the second, and the second for the adult phase. In the absence of the crucial test of experiment,

the evidence points to the inheritance of the form and details of grouping, as well as to that of pigmentation.

Palæmon.—The same is true of many other Decapods. Prawns, for example, though they may become redder in deep water than in shallow, have a constant pattern. Their ordinary colouring is no clear index of their possibilities. Usually they range from a semi-transparent grey tint to deep brown with yellow markings; but, under special stimulation, the stores of dark pigment which they usually keep in reserve, even if exposed to a dim light in dark surroundings, can be called forth, and they then assume an excessively dark tint. In deep water it is probable that either there is rapid transformation of yellow pigment into red, or of deep red into light red, or merely a selective effect, the red pigment alone exuding from the branches, whilst the yellow and blue, to which, as well as to the red, the above black effect is due, remain contracted.

The system of chromatophores which effects these changes is largely determined at birth. We pointed out in a previous section that the secondary system of chromatophores, *i.e.*, the elements of the effective colour-pattern, is established in *Palæmon* even before birth. The foundations of the stripes across the carapace and pleura are laid in the embryo (Plate 22, figs. 33 and 34), and the development of this pattern in spite of the various conditions under which the later larval and adolescent stages are passed, serves to emphasise the definiteness of the chromatophore-system and the independence of the form of this system from the influence of the environment: though it is highly probable that the amounts of red, yellow, and blue pigments, and the share they respectively take in the average colour-pattern, is influenced by the surroundings under which the later development of the shrimp and prawn are passed. The general conclusion, however, is clear: the arrangement or form of these condary system, and to a certain extent the colour-pattern itself, appear to be inherited.

Hippolyte. (Plate 23, figs. 41–50.)—The two cases we have now discussed have this feature in common: the average colour-pattern of the shrimp and of the prawn is constant, and the development of the secondary chromatophore-system is directed to the production of this pattern. In *Hippolyte* the problem is much more complex.

We have described the development of the colour-pattern in three species (*H. cranchii*, *H. gaimardii*, *H. varians*). In the first two the pattern is constant; in the last it is excessively inconstant. The larval pattern is identical in the three species, with the exception of but one or two minute details. They start, therefore, from a common point and reach widely different end-results. But the attainment of the result is not accomplished by a gradual uniform process as in *Crangon* or *Palæmon*: there is, as it were, a second larval colour-phase and thereafter the adult pattern is attained. If we take *H. cranchii* first, the problem can be stated more concisely.

The chromatophore-system of the zoea of *H. cranchii* is identical with that of *H. varians* if we except one single centre. The later development up to the adolescent stage is unknown, but as a minute form, 3–4 millims. long, it occurs among weeds along with *H. varians.* It is then a "lined form," that is to say it has a well-marked ventral stripe due to the neural group of chromatophores, a dorsal line due to the visceral group, and cross-stripes which are in part the caudal chromatophore branches and in part secondary chromatophores developed from, or in close relation with, the caudal ones. The colouring of this lined form is green or red. This adolescent pattern is entirely different from the characteristic colour of the adult, which consists of cross-bars of a sandy tint on a reddish ground. The adult lives, as we described, beneath stones, at least during low-tide. The change from the adolescent weed-haunting habit to the more cryptozoic one of the adult is accompanied therefore by a very great change in coloration, but the new pigment and bars of colour are purely superficial and are laid over the stripes and bars of the adolescent form. Hence in *Hippolyte cranchii* we have—

1. A constant zoeal chromatophore-system and an ineffective though constant pattern.
2. An adolescent colour-phase of bars and stripes ("lined-form"), coloured red or green.
3. A constant adult coloration consisting of broad surface-bars of sandy colour.

If, by contraction, the adult scheme is withdrawn, the adolescent phase is revealed; and if this be examined, the zoeal pattern is still traceable. The primary system persists, the adolescent secondary system persists. Both are hidden under a cloak of constant cut and colour.

Hippolyte varians.—With this species we encounter the problem of inheritance or acquirement of the colour-pattern in its most complex form. It is well known that individuals referable by the usual taxonomic "points" to this "species," offer not only the most bewildering variety of colour and colour-pattern, but it is also known that each individual is capable of changing colour in the course of less than a minute. This capacity is certainly limited in range, but a rapid change of some extent is always possible. This temporary change, however, we know to be quite unimportant, since the form of the chromatophore-system, though variable individually, is constant in each specimen, and therefore we must consider the varieties of *H. varians* from the point of view of variety of form of the colour-pattern. If we do this, we find that there are at least four well-marked form-varieties: the "blotched" form, the "monochrome," the "barred," and the "lined-form." The first, specially associated with the "fascigerous" variety of this species of *Hippolyte,* is distinguished by superficial bands, bars, stripes or spots which stand out in relief against the deep-lying pigment. The "monochrome" may be red, green, or brown, and its colouring is due to an intricate surface network or to minute closely-set centres whose branches interlace without a network necessarily arising (Plate 23, fig. 47).

The "barred form" is one in which across the liver-region and across the third or other segment of the tail and tail-lobes a transverse bar of colour extends, whilst the interstices are comparatively free from pigment (Plate 23, fig. 46). The "lined-form" is a colour-variety of *Hippolyte* with dorsal, ventral and intestinal stripes crossed superficially and more deeply by bands in the tail-segment and in the carapace, and with a more dense collection of pigment around the liver. These blotched, monochrome, barred, and lined colour-forms are but a few of the multitudinous varieties; they occur equally in males and females, but are less clearly defined in the former. [Coloured figures of these varieties are given in our paper (1900.)]

Whatever the colour of the female may be, the chromatophore-system of the zoea is uniform. The only difference that we have detected in the progeny of differently coloured parents is a slightly varying amount of red pigment. The progeny of females with much red pigment have, so far as our breeding experiments go, more of the substance in each chromatophore, than have those derived from green parents in which red pigment is less abundant. But the number and size of the primary and secondary chromatophores of all zoeæ are constant: and, since the yellow reflecting substance is more effective than the red (if we can use the word effective where only a grey or greenish-yellow tint results), even this slight difference between the progeny of differently coloured parents can scarcely be of much consequence in the future history.

The next stage we have been able to investigate is the adolescent stage (3–4 millims. long), when *Hippolyte varians* has passed through the *Mysis*-stage, abandoned its pelagic life, and adopted the habit and form of the adult. The youngest of these show three distinct modes of coloration, "lined-forms," "barred," and "monochrome" forms. "Lined-forms" are exceedingly abundant, and are almost transparent, faintly marked with brown, when seen by transmitted light, and by dots of yellow by reflected light. Others are marked with red down the dorsal and ventral surfaces and along the gut. Others are similarly striped with yellow or green.

The coloration of "barred" forms is due to a disposition of chromatophores similar to that which gave rise to this colour-form in adult *Hippolyte*.

"Monochrome forms" are again due to the same arrangement which we have described in the adult.

Thus the first adolescent patterns are identical with those of the adult patterns, and underneath each of them the constant primary system can be discovered; in fact, the faint brown-lined colour-form is to all intents and purposes merely the larval pattern writ large. But for one class of evidence, the conclusion would seem to be that in these adolescent colour-forms we have the chief varieties of adult *Hippolyte*. This evidence concerns the second adolescent patterns.

We saw in *Hippolyte cranchii* that the adolescent "liner" assumed the adult coloration by the development of a superficial cloak of pigment. In *H. varians* the liner may persist without any concealment, or it may be covered by a coloration very

similar to the one constantly adopted by *H. cranchii* (Plate 23, figs. 48 and 49). Similarly, the barred form may persist or may become concealed. In these ways the blotched colour-form of adult *Hippolyte* arises. Such, however, are not the only possibilities open to lined and barred forms. By the development of scattered superficial centres a "lined-form" may become a monochrome. By the filling up of previously translucent spaces, the barred form may also become a monochrome, and in this case the interstitial chromatophores may be deep or superficial or both. But a monochrome colour-form has to persist and can but modify its surface by the development of spots of reflecting substance.

We may summarise the different paths along which *Hippolyte varians* travels in the following way:—

1. *Zoea.* Chromatophore-system constant.
   - *a.* Primary.
   - *b.* Secondary.
2. *Mysis*-stage unknown.
3. First adolescent colour-forms.
   - *a.* Lined-forms. May be almost colourless, red, brown, green, &c.
   - *b.* Barred-forms. Usually brown.
   - *c.* Monochrome forms. Brown, green.
4. Second adolescent colour-forms.
   - *a.* Persistent lined-forms.
   - *b.* ,, barred-forms.
   - *c.* ,, monochromes.
   - *d.* Lined-forms metamorphosed into blotched forms.
   - *e.* ,, ,, ,, monochrome forms.
   - *f.* Barred-forms to blotched.
   - *g.* ,, to monochrome.
5. Adults.
   - *a.* Persistent lined-forms.
   - *b.* ,, barred-forms.
   - *c.* ,, monochromes.
   - *d.* Blotched forms $\left\{\begin{array}{l}\text{originally lined-forms.}\\ \text{,, barred-forms.}\end{array}\right.$
   - *e.* Monochrome $\left\{\begin{array}{l}\text{persistent.}\\ \text{originally lined-forms.}\\ \text{,, barred-forms.}\end{array}\right.$

Throughout this varied history the primary, centralised system, begun in the zoea

and completed in essentials in the later larval stage, persists. It is plain in liners, in barred-forms and in blotched forms; but is less distinct in monochrome colour-forms, particularly in green *Hippolyte*.

The first adolescent liner is a colour-form largely due to the primary system aided by a feebly developed secondary system. In all other adolescent forms, the secondary system is the dominant factor.

The adult pattern may arise simply from a persistent first adolescent form (liners, barred-forms); or from these, altered to monochrome colour-forms, either by the addition of deep chromatophores or of superficial ones or of both, to those already existing. It is independent of the larval, *i.e.*, the primary, system. It may be independent of the adolescent secondary system, since, as we have shown, apparently identical monochrome-forms result from very different starting points. In short, the adolescent patterns, limited and well-defined though they be, are not so many starting points from each of which a number of definite colour-patterns ultimately arise, nor does each necessarily persist; they are so many skeletons which the environment may tolerate (adult liners and barred colour-forms), or which it may clothe and hide, and it is a matter of indifference which form of skeleton is chosen; the trappings supplied by the environment may produce the same external appearance (monochrome) no matter on what form they be hung.

These considerations lead us to conclude that the primary system of chromatophores in *Hippolyte varians* is inherited; that the evidence on the primary adolescent colour-patterns does not permit us to decide whether they are inherited or acquired; that whether inherited or acquired, these early adolescent patterns are often without significance in the final colour-display. The adult pattern arises in spite of difficulties which are thrown in its way. Gaps are bridged over, stripes are evolved, stripes are made to bars, and bars blend to a monochrome. The hundred forms of *Hippolyte* arise, even though the original plan of the adolescent colour-variety has to be so supplemented as to be almost abandoned. On these grounds we conclude that the adult colour-pattern of *Hippolyte varians* is determined by the environment and not by inheritance. We venture to go further, and to suggest how this extraordinary influence of the environment may act.

We know (see Section IX.) that the pigments of the chromatophores expand into the branches under certain conditions of illumination (*e.g.*, on dark background) and contract into the centres in diffuse light. Imagine a practically transparent *Hippolyte* (such, for example, as the earliest adolescent faint brown-lined forms) resting persistently, as it does rest, in such a situation that a bar of shadow falls across it, whilst over all the rest of its body light falls. In the region of the bar of shadow the chromatophores will expand. In the rest of the body they will be contracted to mere dots. Grant that, where the conditions are favourable to the activity of the chromatophores, growth will be greater than when its contents are aggregated in the manufacturing centre—a supposition which is no more unreasonable than that

which supposes that functional activity favours growth. Then, in the region of shadow, new chromatophores are formed either by budding from, or in relation to, an existing centre. These in turn give rise to new centres in a like manner. The bar of shadow is now reflected on the surface of the animal by a bar formed of chromatophore-branches. *Hippolyte* has grown into its surroundings.

Further, if we accept a recent explanation of absorption-colour-photography, we can see how the colour of this bar of shadow comes to resemble that of the object that casts it. For WIENER has shown (1895), that a combination of substances may exist, so sensitive to light as to be decomposed thereby, and give rise to a pigment of the same colour as that of the incident light. If we postulate such a substance, or combination, in the chromatophores of *Hippolyte*, then the bar which we have just seen produced will be of the same colour as that of the object which throws the shadow. We may thus picture the mode whereby *Hippolyte varians* become infinite in variety.

It will be clear that every step in the development of these colour-patterns in *Hippolyte* carries with it certain disabilities. A reversal of the conditions which have called forth that development will not, once the development is completed, evoke a regression, and so we shall not expect to find a monochrome colour-form reverting to a "liner." Moreover, if the hypothetical sensitive substance is not the pigment itself but the mother of pigment, we shall not expect to find that change of light-conditions will readily produce the permanent change of coloration. The pigments first formed hold the field against later comers. This is absolutely what we do find. It was only with extreme difficulty that, for example, we were able to convert a green *Hippolyte* into a brown ('Quart. Journal Micros. Sci.,' vol. 43, 1900, p. 614).

Lastly, though we conclude that the final colour-pattern is due to the influence of the environment and not, as in the shrimp and prawn, to heredity, yet, even in *Hippolyte*, heredity plays a part; it provides points of departure for the formation of these adult patterns; and through the general symmetry of the body, limits the arrangement of bars, stripes, and spots of colour to certain regions and in relation to certain structures.

Summary.

1. The colour-pattern in Mysidæ is the effective expression of the more superficial part of the dominant primary chromatophore-system. Though crucial experimental evidence is wanting, we conclude that this primary system and its resulting colour-pattern are inherited.

2. In certain Decapods (*Crangon*, *Palæmon*) the adult colour-pattern is constant and is the expression of the dominant secondary chromatophore-system. From the embryo to the adult, the development of this system is devoted to the increasingly complete expression of this constant pattern, underneath which the persistent primary system can be recognised. We conclude that both the primary and secondary systems and the colour-pattern are inherited.

3. In other Decapods (*Hippolyte*) the colour-pattern is either constant (*H. cranchii*, *H. gaimardii*), or inconstant (*H. varians*); but in either case is the expression of a dominant secondary or even tertiary system of chromatophores. In all three, the larval pattern is closely similar. But this pattern counts for little in the production of the adult pattern which, unlike that of the shrimp, is not gradually developed. One or more adolescent patterns are first formed, which are so many skeletons which the environment may tolerate (adult "lined forms" of *H. varians*); or which it may clothe and hide (*H. cranchii*, most colour-forms of *H. varians*); and, in the production of the "monochrome" colour-form of *H. varians*, it is a matter of indifference which of these adolescent patterns is chosen.

We conclude that in all these *Hippolyte* the primary system is inherited, and that in *Hippolyte varians* the ultimate form of the secondary system, the adult pattern, is due to the action of the environment.

SECTION VI.

The Taxonomic Value of the Chromatophore-system.

(Plates 18–21 and Plate 23, figs. 51–2.)

The prevalent opinions that chromatophores are sporadic cells filled with pigment, that the colour or pattern they produce is inconstant, and that colour is protective or valueless, have prevented naturalists from using chromatophores or colour-patterns for purposes of classification.

We have shown that, throughout certain Mysidæ and Decapods, a system of organs, the chromatophore-system, occurs with unfailing regularity. The chief part of this system, the primary system, is distinguished by its form, grouping, and adherence to segmental type. In Mysidæ, this is confined to the central plane of the body, and a small part of it is specialised to form a peripheral group, the beginning of the secondary system. In Decapods, the secondary system springs from this and many other isolated origins, and a decentralised system is the result. Yet, under this covering, the persistent primary system can be discovered, with the characteristic Mysidean feature of form, grouping, and segmentally-arranged centres. It is useless as colour; it gives rise at most to but a fraction of the effective system. The possession of this primary system in both Mysidæ and Decapods, appears to us to have as good a title to taxonomic value as the arrangement of the appendages upon which the association of these two groups is based.

To test the value of the primary system in this sense we have examined *Nyctiphanes*, one of the Euphausiid Schizopods, and *Anaspides*, a Crustacean which appears to connect Schizopods with Decapods and Amphipods. We find in *Nyctiphanes* a typically Decapod arrangement, and, though the specimens at our disposal were not fresh, we identified a scattered system of chromatophores on the

carapace, tail and limbs, and traces of a centralised system on the ventral surface of the body and on the stomach.

Up to the present time, the Euphausiidæ have been generally regarded as nearly approaching the ancestral form, from which on the one hand Decapods, on the other Mysidean Schizopods, have developed. The evidence of the chromatophore-system was opposed to such a view and favoured the inclusion of Euphausiidæ among Decapods.

It was, therefore, with satisfaction that we heard that Dr. HANSEN of Hamburg had arrived at exactly the same conclusion after a prolonged study of the appendages. His evidence has not yet been published, but he kindly allows us to make this statement. In this case, therefore, the chromatophore-system, as a taxonomic instrument, has proved to be of considerable value.

We may next take the case of *Anaspides.* This peculiar Crustacean, found chiefly in a subterranean water in Tasmania, has been examined by Mr. G. M. THOMSON (1894) and Dr. CALMAN (1896). In particular, the researches of the latter have rendered the position of *Anaspides* one of great interest to carcinologists. Dr. CALMAN has pointed out that *Anaspides* is probably a synthetic type of a kind met with in Palæzoic rocks. It combines with a Schizopod's feet, a Decapod auditory organ ; like Amphipods or Isopods it has no carapace, and yet possesses stalked eyes. Thanks to Professor HOWES and to Dr. CALMAN, we have been able to examine preserved specimens of *Anaspides*, and we have found traces both of a centralised and of a peripheral system of chromatophores (Plate 23, fig. 52). Opposite to the base of each pair of appendages and closely applied to the nerve-cord, there is an unpaired chromatophore-centre from which long branches run up the body-wall and down the endopod of the limb, very much as in *Mysis* the branches of the neutral group of centres supply these two organs. In fact, this is the neural group. It is centralised, segmental, and has the far reaching branches of the Mysidæ. In addition to these chromatophores, there are hexagonal plates of pigment on the skin of the abdominal pleura, and more deeply placed pigment-masses in the mid-dorsal line of each segment. The former appear to be superficial deposits of pigment and not chromatophores, the latter may be caudal centres, but are not sufficiently well-preserved for us to pronounce upon them. The presence, however, of a neural group suggests affinity with *Mysis,* whilst the presence of scattered apparently functionless pigment-spots might be taken to indicate a Decapod or Amphipod character. In the absence of living specimens, it is difficult to describe or define the characters of the chromatophore-system more fully, but the conclusion that the system shows a Mysidean character, agrees with that drawn by Dr. CALMAN from a study of the appendages, though in some characters it is to the Euphausiidæ rather than to the Mysidæ that *Anaspides* shows affinity. A further study of the chromatophore-system, carried out on fresh material, will probably yield evidence on this head.

As a guide to generic and specific characters, the primary system has high claims. We have seen that each genus of Mysidæ that we record, has its own modification of this system; except *Schistomysis*, which is inseparable from such *Macromysis* as *M. inermis*, and there are grave doubts of the validity of *Schistomysis*. It was separated from the old genus *Mysis*, chiefly on account of the long bifid appendage on its fourth abdominal segment in the male. If only females are taken, it is difficult to refer them to this genus. Further, since a similarly modified male appendage occurs on the fourth segment in *Hemimysis*, it would appear that even this character is not peculiar to *Schistomysis*. In fact, the division of many old genera into new ones, and the validity of critical species, are often based on characters of sex or on points that may change during the growth of an individual as much as they may differ in two specimens of the same age.

In place of these variable characters, or in addition to them, we suggest that the study of the chromatophore-system may give results more easily recorded and more soundly based. The form of the centre-system in which we find generic characters, and the details of this and of the branch-systems which define the species, are characters that arise early in life, are constant in both sexes, and persist unchanged.

As an example of the constancy of this centre- and branch-system, we may refer to the result obtained on the commonest marine *Macromysis*.

It is held by SARS and NORMAN* that there are two close-allied species of this genus, *M. flexuosa* and *M. neglecta*. The distinguishing characters are such that only adults can be satisfactorily determined. *M. neglecta*, however, has on the average a smaller number of tarsal joints and a shorter antennulary peduncle, as compared with its antennary scale. In fact, it is altogether a smaller animal than *M. flexuosa*. The differences appeared to be largely explicable as stages of growth of one form. Most systematists have, however, found it impossible to identify specimens of *Mysis* with *M. neglecta*.

We have examined the chromatophore-system and find that in specimens referable to *M. flexuosa* two clearly distinct types of centre- and branch-systems occur. Each breeds true. Each possesses before birth its own system of centres and branches, which persist throughout life in both sexes. The chief difference is that in one type the neural centres are paired throughout the thoracic region; but only occur opposite to the third, sixth and eighth appendages in the other type. The first type we call *M. flexuosa*, the second *M. nigra*. The reason for retaining the name for the first type is because the first figure† of "cancer flexuosus" shows the chromatophores to be of that type.

We have recently obtained a mature male specimen of *Macromysis* which agrees in

* Reference may be made to a paper by HOLT and BEAUMONT (1900), in which the opinion of these authors is discussed.

† O. F. MÜLLER, 'Zool. Danica,' Plate 66. fig. 2 (Ed. 1788, Folio).

every detail with *M. neglecta.* This specimen had the neural centres of the *Nigra*-type. Hence we conclude—

1. That *Macromysis flexuosa*, AUCT., contains a mixture of two species.
2. That *M. neglecta*, SARS, is simply the mature, but not fully grown condition of one of them, namely, *M. nigra*, n. sp.
3. That, to prevent future confusion, the name *Flexuosa* be given to the form whose centric system is strongly developed and present in each thoracic segment; that the name *Nigra* be given to the form which has centres on the third, sixth and last choracic, and that the name *Neglecta* be dropped.

The figures 1–6, 10–12, 16–18, on Plates 18, 19 and 21, illustrate fully the characters of each form.

The value of the chromatophore-system is not confined to the identification of adults. Perhaps its chief use is in the discrimination of larvæ.

We have seen that in the development of Decapods, the zoea of each form hatches with a perfectly constant supply of chromatophores. In each species of *Palæmon, Hippolyte* and *Crangon* that we have examined, the larva has one or more distinctive centres. The secondary as well as the primary system is constant, both at the early and late larval stages. The branch-system and pigmentation offer other distinctive features. The great taxonomic importance of the primary system lies in the fact that the zoea of each species breeds true, and that the resulting primary system is retained.

SECTION VII.

THE STRUCTURE, RELATIONS, AND SIGNIFICANCE OF THE CHROMATOPHORES.

(Plates 21 and 22, figs. 19–23A.)

Very few attempts have been made towards elucidating the structure of the chromatophores of Crustacea. MAX WEBER (1881), HALLER (1879), MATZDORFF (1884), and MAYER (1882) have studied them in Isopods. POUCHET (1876) has given an account of them in the shrimp; WAGNER (1896) and NUSBAUM (1897) have described them in *Mysis.* In all these cases, the chromatophores have been investigated incidentally rather than specially; and the morphological and physiological problems which they present have scarcely received recognition, much less solution. Though generally considered to be isolated stellate cells, POUCHET showed that associated cells, each differently pigmented, occurred in *Crangon*; WAGNER and NUSBAUM figured multicellular structures in *Mysis.* The only account of their development is the statement by WAGNER, that in *Mysis* the "Pigment-drusen" arise from the epidermis.

1. *Structure of the Chromatophores.*

A. *Mysidæ.*—We may recapitulate the chief points of the structure and development of the chromatophores of *Macromysis flexuosa*, to which we have referred in Sections II. and III., and figured in Plate 22. Each of these organs is composed of a granular and slightly fibrillar central cytoplasmic body, bounded by a distinct membrane. From this " centre " the branches emerge at first as thick trunks forming further outwards fine ramifications. In the chromatophores of the telson, the proximal end of each branch is a single cell projecting somewhat into the central sac, and dividing peripherally. In the chromatophores of the blood-lamellæ, four or five nuclei are found in the trunks, and there is no clear separation of a central sac from the cells which form the branches. In the neural and caudal groups of primary chromatophores, the nuclei are again more central in position, and the centre is largely formed by the fused proximal ends of the branch-cells.

The chromatophores of the neural group develop as vesicles at the expense of the epidermis covering the embryonic ganglia. Each vesicle consists of about a dozen cells ranged round a central cavity into which they secrete pigment. Subsequently, the chromatophore grows inwards between the successive ganglia, and forms a curved C-shaped organ. The cells elongate, and form the branches. Later still, the centre divides, one part separating to supply the flexor muscles, the other, sending branches to the ganglia, nerves, and appendages.

The structure of the different parts of the Mysidean chromatophore requires further consideration, although we are not able to offer a complete solution of the many problems which they present. We have already noticed that in different regions and in different stages of growth the appearances of the chromatophores are by no means the same. We have now to add that in addition to the nuclei at the basal ends of the branch-cells, elongated fusiform nuclei are frequently found in rows along the more peripheral part of the branches. We are inclined to regard these as belonging to cells, the bodies of which have formed, or become converted into a sheath. All the appearances we have seen go to show that the branches, whether unicellular or not, are tubular, the wall of the tube being composed either of the enveloping cells just described, or of the outer substance of the branch itself. The arborisations and exceedingly dense, filmy, plate-like extensions and terminations of the branches are tubular also. The pigment returns to the same pattern time after time.

With respect to the mechanism of the movement of pigment, we can only speak with uncertainty and diffidence. The view adopted by POUCHET was that of active amœboid movement of cell-processes. Direct and convincing evidence of this still prevalent view, we have failed to discover. We, therefore, feel ourselves at liberty to suggest rather that changes in turgidity of the constituent cells of the centres effect the expansion into, and contraction from, numerous fine ramifications which arise from

the main branch, than that these movements of the pigments are due to amœboid movements in the plasma therein. We have some slight evidence that the pigment movements are due to a pressure from the centre, inasmuch as in old Mysids the pigment at times bursts the frondose extremities of the chromatophores, and exudes into the surrounding tissues. Light is known to set up changes in the turgor of such chlorophyll-containing cells as the guard-cells of stomata. We know that light sets up movements of the pigments by its direct action on the chromatophores (Section IX., pp. 351–353), and suggest, not as an ascertained fact, but as a subject for further experimentation, that pigment movements are due to changes in turgor of the chromatophore-centres; which changes may be produced by the direct action of light, and also by the nervous system.

Whatever view we take of the finer details of structure, and of the mode of working of this organ, its complex structure, glandular secretory activity, the power of growth and increase in size and number of its individual "cells," is beyond question. All the Mysidæ we have examined present a similarly organised system of chromataphores.

B. *Decapods.*—In spite of long-continued and renewed attempts to resolve the structure of chromatophores in Decapods, we have only partially succeeded. In the zoea of *Hippolyte*, the primary centres are multinuclear organs, from which the red absorbing pigment and the yellow reflecting substance can be extracted, leaving vacuolar spaces in their stead. In adult *Hippolyte*, the chromatophores lie in the connective tissue, and their centres consist of nests of nuclei lying in vacuolated protoplasm. Flattened, spindle-shaped nuclei occur along the course of these branches, and the cell-bodies belonging to them have contributed to the branch either as its continuation, or as a sheath. In the shrimp, the majority of the chromatophores are confined to the deeper layers of the skin, whilst in *Hippolyte* and *Palæmon* there are exceedingly rich development in the muscles. These intermuscular chromatophores are composed of delicate tubes, some of which join centre to centre, and others form peculiar cribriform stellate endings (Plate 22, fig. 23A). The chromatophore-branches of Decapods are not only much shorter than those of Mysidæ, but they do not exhibit the filmy arborisations in which the Mysidean chromatophores terminate. In the muscle and skin of *Hippolyte*, however, the branches of the chromatophores subdivide into a network of very fine mesh; adjacent chromatophores run together, and lose their individuality completely. Under these circumstances their pigments produce a very vivid effect. Nevertheless, under suitable stimulation these networks break down; the pigments aggregate into definite centres, and a transparent, colourless condition results. These appearances can be repeated on the same tissue, and offer the same problem that we discussed in *Mysis*. We cannot translate these phenomena into terms of the cell-theory; but we know that though not necessarily originated, these movements are controlled by the nervous system; and subsequent research will have to decide whether amœboid

movement or turgor is the agency under which these migrations of pigment to and from ramified channels of great extent, are carried out.

2. *Relations of the Chromatophore-system.*

A. *Mysidæ.*—We have already pointed out that the position of the chromatophore-centre is no index to the extent of its relation to the body. The neural centres are placed at the sides of the nerve-cord, but their branches run in relation with all the chief organs of the body. The visceral group of centres, on the other hand, only supplies the gut, gonads, and part of the carapace: the caudal group, the skin, and extensors of the tail. The accessory centres are limited to the tissue immediately round them. We propose to consider these relations of the centres and branches more fully than we have done in the previous sections.

There is an unmistakable relation between the chromatophore-centres as a whole, and the nerve-ganglia. The neural centres are developed in close connection with ganglia. Their branches form, especially in *Macromysis inermis* (Plate 20, fig. 7, and Plate 21, fig. 16C), a complete sheath to the central and peripheral nervous systems. The special organs of sense, eyes, antennæ, tail-lobes, otocysts, have a special accessory group of chromatophores. The neural group is the most constant, the most highly-developed, and the first to arise.

The visceral group is also related to the nervous system through the stomogastric system of nerves and ganglia; and both this and the caudal group occur in positions where NUSBAUM (1899) has found peripheral ganglion-cells, *e.g.*, on the great vessels and in relation to the heart.

In addition to this nervous relation of the centres and branches, the chromatophores are intimately connected with other organs of the body. We have described (Sect. II. D, pp. 304 and 305) the glandular tissue that is constantly associated with the chromatophores of Mysidæ; the dense ramifications and plexuses formed by the branches of the neural chromatophores in the muscles and skin; the arborisations of the caudal group in the skin and extensors of the tail; the close fitting network round the liver-lobes, the gonads, upon the upper surface of the stomach and intestine and to a slight extent upon the carapace. The chromatophore-branches thus ensheath the organs of the body of Mysidæ.

B. *Decapods.*—The persistent primary system of chromatophores in this division of Crustacea exhibits the same fundamental relation of its centres to the nervous system, to the glandular system and to the skin, that we have just described in Mysidæ. As in the latter, the neural group is the most strongly developed, and in many instances (maxillary chromatophores of *Palæmon*, of *Crangon*, of *Hippolyte* and abdominal centres of *Crangon*) form elaborate, far-reaching branches that supply muscular and dermal organs.

This centralised primary system is, however, dominated by the scattered secondary

system of chromatophores. The place of the all-pervading branches of *Mysis* is now in *Hippolyte* taken by small centres and restricted branches. These secondary chromatophores arise in groups, some of which are related to the primary groups and supply the same organs. Others arise independently at the base of the gills in the carapace and in the limbs where no primary centres are met with.

In *Palæmon* and *Hippolyte*, the secondary system may be said to be fully developed, since its elements accompany the connective-tissue sheaths and partitions of all the organs and penetrate between the cells of the epidermis. In *Crangon*, the centre-system is chiefly restricted in the body to the skin and tail-flexors. In the crab, the pigment is confined to the dermis and epidermis. The varying extent of the secondary system in Decapods and its more or less intimate relationship to the body as a whole will have to be determined by future research. We know that chromatophores occur in almost all groups of Crustacea, but their structure, movements, and arrangements have been hitherto very superficially examined. When this is done we shall be in a position to discuss the evolution of the system in the group as a whole. In the present paper we have to content ourselves with the examination of a few isolated cases.

The Nature of Chromatophores.—Almost all previous observers have considered chromatophores to be amœboid cells capable of temporarily uniting together by their processes and subsequently separating to their respective centres (MATZDORFF). POUCHET, however, found that three to four cells, each with its own specially coloured pigment, formed a single colour-element in the shrimp, but he regarded each cell as functionally independent of the rest. We have seen, however, that in Mysidæ and in Decapods the evidence goes to show that both the primary, and at least some of the secondary, chromatophores are not aggregates of really separate amœboid cells of connective tissue nature. The chromatophores are polynuclear stellate masses of cytoplasm, the central part of which is bounded by a distinct membrane and the fibrillated branches have also for a greater or lesser part of their length an envelope which gives their path a permanent and a tubular appearance. At the base of each branch, one or more large nuclei are present within or just without the central envelope. Peripheral flattened nuclei are also present.

Each pigment has its own branch-system and its own share of the centre. By a mechanism, the nature of which is still obscure, the pigment can be contracted to a central ball or distributed in a definite pattern along certain branches; the result varying according to the nature of the stimulus, the colour of the pigment and, to some extent, the age of the animal. The basal and nucleated parts of the branches are in all probability the seat of a pigment-manufacture which is begun in the primary system during embryonic life, in the secondary one at different stages, but is continued in all chromatophore-centres throughout life. In some Crustacea, this results in the accumulation of pigments; in others, the first-made substances are transformed into a soluble form, distributed (as for example, the nocturnal blue substance of *Hippolyte*) in an independent system of spaces throughout the muscular and other tissues, and is

probably destroyed in these spaces by the action of light. Concomitantly with this transformation and destruction, a change of chemical reaction occurs (Section VIII., pp. 341–343). The chromatophores are therefore a system of organs, often complex in structure; intercommunicating and united functionally with one another, and with the eye, by the mediation of the nervous system; constantly manufacturing, and storing or transforming pigmentary substances; and playing an important part in metabolic change.

The origin of such a system is not to be found in sporadic stellate cells of the connective tissue. It is to be sought rather in a glandular tissue with a definite topography. In support of this conclusion we urge (1) the secretory activity of chromatophores; (2) their definite grouping, segmental arrangement, and discontinuous variation in Mysidæ; (3) their special topography in Decapods, in which group the primary system persists and the secondary scattered one arises; (4) their structure and development; (5) their relation, in Mysidæ, with a glandular tissue.

Our knowledge of the cutaneous glands of Crustacea and especially of Schizopods is too inadequate to permit us to pursue this line of phylogenetic research. We may, however, point out that the special development of chromatophores on the mouth-parts of larval and adult Crustacea, the segmental arrangement of neural and caudal groups, and the special connection of secondary chromatophores in Decapods with the gills and carapace, may receive a natural explanation if their glandular antecedents have (as is known to be the case in the oral and branchial regions) had a restricted distribution. The figures and description by HERRICK (1895) of the tegumental glands in the Lobster, and by ALLEN in *Palæmonetes* (1893), show that the glands consist of epidermal cells bounding a frequently pigmented cavity which communicates with the exterior by a duct. We have shown that in the neural chromatophores of *Macromysis flexuosa* the same mode of origin applies. The comparison is incomplete in that the chromatophore loses its connection with the surface and acquires the power of exhibiting pigment migration, as well as pigment-formation. Nevertheless, highly specialised as are the chromatophores of Mysidæ and of Decapods, they exhibit a structure and development, an activity, a topography, and a relation with undoubted glandular tissue that points to their origin from organs of a glandular type.

SECTION VIII.

THE BLUE PIGMENT OF *Hippolyte varians* AND OF *Macromysis nigra*: THE TISSUE-REACTIONS OF THESE CRUSTACEA.

We have shown in a former paper that certain Crustacea, *e.g.*, *Hippolyte varians*, owe their coloration to red, yellow and blue pigments; that the red and yellow pigments are, in the main, responsible for the diurnal colour, whilst the blue alone produces the nocturnal colour. We have shown further that the yellow pigment reacts most rapidly to light-stimuli, that the red pigment reacts less rapidly but in

the same way; and that the light-conditions which induce a contraction of these pigments into their chromatophore-centres, induce also an expansion of the blue. The blue (nocturnal) phase may be called forth either by darkness or by exposing *Hippolyte varians* to scattered white light, *e.g.*, in white porcelain dishes (white background effect); or in clear glass dishes into which sea-water is poured with sufficient violence to produce and maintain a foam.

In this section, we bring forward facts which enable us, as we think, to carry our knowledge of the significance of these pigments and pigment-changes, a step further forward.

When appropriate light-stimulation is provided, the red and yellow pigments flow out from the chromatophore-centres along definite channels. In some Crustacea, *e.g.*, *Macromysis flexuosa*, *M. inermis*, &c., these channels, the branches of the chromatophores, may be seen clearly in the living animal even when all pigment has withdrawn from them into the chromatophore-centres. In *Hippolyte varians* and allied species the branches of the chromatophores are much finer and are only easily visible when they are naturally injected with their pigments.

The nocturnal (blue) pigment of *Hippolyte* only expands when the red and yellow pigments contract: that is, when they flow back into the chromatophore-centres from which the blue escapes. The blue pigment does not flow along definite channels, at least not entirely, but spreads as a fine suffusion from the centres, sometimes forming a delicate reticulum, sometimes blue "halos," and sometimes lump-like aggregations about them. The lump-like aggregations may persist for some time without apparent change even when the light-conditions are such as to induce a re-expansion of the red and yellow pigments; that is, a resumption of the diurnal coloration. In some colour-forms of *Hippolyte varians*, permanent aggregations, "blue spots," occur. Beyond the borders of the blue halos produced by the suffusion of pigment from the centres, the blue colour gradually fades away, nevertheless the nocturnal blue colour of the animal is due to the delicate blue of this out-lying pigment, the halos being, like the chromatophores themselves, too minute to impress the naked eye.

Blue pigment is occasionally expanded during the day and then contributes to the diurnal hue; thus the green colour of *Hippolyte* taken from *Zostera* is the optical effect of a yellow network mixed with blue, the red pigment being contracted. Blue pigment may occur in an expanded form under such different light-conditions, *e.g.*, in normal green diurnes, in nocturnes (in darkness), in light-induced nocturnes (white background effect), that we cannot regard its movements as being controlled by light as those of the red and yellow undoubtedly are.

We have seen that the red and yellow pigments flow back in due order into the chromatophore-centres in obedience to light-stimulations, and that the blue issues from these centres. If this exudation of blue is not a light-effect, it seems to us probable that it is a consequence of the contractions of the light-sensitive pigments (the red and yellow). The diffuse condition in which the blue extrudes, its occurrence

outside the regular branches, its exit from the centres following on the entrance of the red and yellow, suggest that the cause of its discharge is mechanical. Discharged, it is gradually washed away from the centres—hence the halos—or aggregates for a time about them. The red and yellow pigments enter and leave their centres as often as appropriate changes of light-condition occur. In the animals in their natural surroundings, these movements of yellow and red pigment take place, as we have shown, at least twice a day, at nightfall and at daybreak. But there is no evidence to show that the blue pigment, once it has left the centre and finds itself outside the branches, may re-enter. It may be likened to a secretion and differs in physical, and probably in chemical, properties from the red and yellow pigments. Moreover, unlike these latter it, except in the case of green *Hippolyte*, plays no protective *rôle*; blueness on dark nights at sea confers no advantages. It must be regarded either as a proivsion for a possible green episode in the colour-history of the animal or as being of no protective value. The former hypothesis meets with no confirmation from such facts as we possess. Many *Hippolyte*, as we know, have no period of greenness. It is with the greatest difficulty that a brown *Hippolyte* can be induced, even after weeks of enforced sojourning on *Zostera*, to make any show of greenness. Therefore we regard the blue pigment as not sharing any such protective function as may be supposed to fall to the lot of red and yellow pigment. Physically it is far more diffuse than these pigments and it is more readily destroyed, for instance, it disappears suddenly when the animal is subjected to a temperature of 60° C. Nevertheless, the blue pigment seems certainly to be related to the red and yellow. It arises in the same chromatophores as these. It appears later than these and increases in amount as they increase. It makes its appearance about the chromatophores in young animals after they have been in captivity for some days or after they have been subjected to high-light intensity. In certain chromatophores of *Hippolyte*, strands of red pigment may give place rapidly to blue strands; the mode of change suggesting a transformation rather than an actual replacement. We conclude, therefore, that the blue pigment of *Hippolyte* is a derivative of the red and yellow pigments periodically discharged from the chromatophore-centres and gradually destroyed or changed in the body of the animal.

The regular nocturnal exudation of blue pigment from the centres, points to the existence of great metabolic activity in these centres. They must be regarded not as a collection of pouches in which the pigments may be kept when not in use; but as glands producing not only pigments sensitive to light, but also a by-product which is periodically discharged. It were easy to suggest that the by-product being blue, might, if it were discharged during the day, interfere with the protective resemblance in the production of which *Hippolyte* seems so adept, and to trace its nocturnal removal and the whole phenomenon of periodicity in *Hippolyte* to this. But this would be to assume the very thing that a protectionist should be asked to prove and which, for our part, we regard as not yet proven, that the whole duty of pigment is

protective. Moreover, as a matter of fact, the superficial network of red or red and yellow, effectually screens any deeper lying colour from view. It is at least as possible that the chromatophore-centres are the seat of changes which result not only in pigment-production but also in its destruction and the consequent manufacture of other substances whose importance, for all we know, may rival that of the pigments themselves. Night after night, every chromatophore-centre in the skin, the muscle, about the gut and liver, discharges its quota of blue substance. Yet there is no accumulation of blue pigment in the body. Therefore it must undergo destruction or at least change. Till we know the nature of this change we must hesitate before giving judgment as to which function of the chromatophore is the more important, the production of pigments giving rise to appearances of a protective nature, or that of the blue substance which is given over to metabolic processes of the body.

The changes in the pigments in *Palæmon serratus* and *Palæmon squilla*, when these animals are transferred from a black background to a white one, offer further support to the view that the blue pigment is a product of the red and yellow ones. The positive colour-phase of these prawns is due to an expansion of red, yellow, and blue pigments, the blue forming an irregular aggregation about the red. If, now the transfer is made, both red and yellow pigments retract into the centres of the chromatophores, leaving the blue expanded. The form of the coloration is retained, but the tint is changed from brown or red to blue. After a short time, however, the blue disappears completely, leaving the animal colourless. If in this negative phase it be replaced in the back background, the expansion of the red and yellow pigments is accompanied by an evolution of diffuse blue. These changes prove the instability of this form of blue pigment, and give further evidence of its origin from the other pigments. This conclusion is also supported by observations on the zoeæ of *Palæmon squilla*. At the time of hatching, these larvæ possess certain chromatophores, each of which contains a red pigment and a yellowish-green reflecting substance. During an experiment with seventy-two larvæ (Periodicity—Table X., p. 371), commenced on August 23, 1901, in darkness, the first record (August 24) showed complete retraction of the red pigments, but with no trace of blue. The succeeding records on August 25 and 26 gave a similar result. On the following day, however, the larvæ had moulted, and reached the stalked-eye stage, and now exhibited a diffuse blue substance about, and exclusively about, the red pigment. In the concluding part of this section, we refer to the occurrence of a similar blue substance in certain Schizopods, and we may point to the close relation of blue and red pigments, which have been deduced by FRITSCH (1891) from observations on *Holopedium*, one of the Daphnids; by HEIM (1892), from a study of several Decapod Crustacea, and by Miss NEWBIGIN (1897), from chemical investigation on the blue pigment of *Astacus* and *Homarus*.

Returning now to the question, "What becomes of the blue pigment"? we must confess that our knowledge on the subject is but scanty. Nevertheless, we set forth

here a series of facts which we have discovered during the last three years, and which are interesting enough in themselves to merit record, even though we should prove to be wrong in thinking that they will throw some light on this question.

The Tissue-reactions of Hippolyte and Mysis.

The nature of diurnal and nocturnal colour-change, from red or yellow to blue; the arbitrary way in which "nocturnes" may behave when subjected to light, now losing their blueness in a flash, now maintaining it for hours; led us to suspect that the pigment changes are not controlled *solely* by the nervous system, but that some other agent co-operates therewith.

The pigment of a chromatophore in an isolated piece of skin of *Palæmon*, or in an isolated limb of *Hippolyte*, reacts with certainty to light-stimulation; yet in the intact animal the reaction of the pigment is at times most uncertain. A nocturne may refuse stubbornly to expand its pigment even though the eye-mechanism is raining down nervous commands upon the chromatophores to do so.

Urged by such considerations as these, we investigated the chemical conditions of the tissues containing the chromatophores during the nocturnal and diurnal phases. Our hope was that we might find in these conditions the cause of the just-mentioned occasional refractoriness of nocturnes to light.

We tested, by means of litmus, the acidity or alkalinity of skin and blood. Finding that rich stores of pigment exist in muscle, and about the liver, we included these tissues in our tests. Subsequently we were compelled also to test the ovaries and the vasa deferentia. The operation of testing samples of skin, muscle, liver, and eggs of an animal was carried out, after a little practice, in about a minute, so that *post-mortem* changes were avoided. We need scarcely say that, when we speak of tissue-reactions to litmus, we mean the gross-reaction of protoplasm plus its accompanying secretions and reserves.

In our experiments we find the blood to be invariably alkaline; the skin almost invariably so; the eggs always acid, and the vasa deferentia alkaline.

On the other hand (see Table, Tissue Reactions, I.), liver and muscle display a remarkable variability in litmus-reaction. Animals, kept under similar conditions, display with respect to these organs, sometimes an acid, sometimes an alkaline reaction, and sometimes both acid and alkaline reactions. Moreover, this variation in reaction of liver and muscle is regular, and, indeed, periodic. (See Tables, Tissue-Reactions, I., II., III.) In the morning, these tissues are generally alkaline, whereas, toward evening, they are acid. Thus, in similar sets of animals, the muscle was alkaline in 95 per cent. in the morning, in 55 per cent. in the afternoon, and in only 44 per cent. in the evening. The liver-tissue gave even more pronounced results, 74 per cent. alkaline in the morning, 53 per cent. in the afternoon, and 35 per cent. in the evening, *i.e.*, 65 per cent. acid at night against 26 per cent. in the

morning (Table, Tissue Reactions, II.). Thus it seems clear that an acid-substance makes its appearance first in the liver and later in the day in the muscle; during the night or very early morning it disappears, in many cases entirely. So, side by side with the nocturnal and diurnal colour changes of *Hippolyte varians*, of *Macromysis flexuosa*, &c., there are also nocturnal and diurnal changes of a chemical nature.

Having made this point, we hoped to have found the object of our search, viz., the disturbing agent responsible for the before-mentioned, occasional refractoriness of *Hippolyte* nocturnes to light.

Since nocturnes were generally acid, and diurnes alkaline, with respect to liver and muscle (Table, Tissue Reactions, IV.), it appeared to us that recovery to diurnal colour-change might be conditioned both by nervous stimuli and by destruction of acid substance (on the assumption that the acid aided in calling forth the nocturnal colour-state).

We tested, therefore, recovered nocturnes (Table, Tissue Reactions, VI. B). These showed, like nocturnes themselves, acidity of liver and muscle-tissues. This, together with the fact that no periodic change of reactions appears in the skin, seems to show that the intermittently secreted acid-substance has nothing to do with the movements of the pigments in the chromatophores of the skin; although it is noteworthy that nocturnal colour-change begins in the liver, then affects the muscle, and finally the skin. If then this strange rhythm of secretions is in any way connected with the rhythm of pigment movement, it must be by acting, not upon the chromatophore-centres, but upon the diffuse blue-pigment after its discharge from the chromatophore-centres.

When we turn to the genus *Macromysis*, *e.g.*, *M. nigra* or *M. flexuosa* (see Section VI.), we find that the alternation of alkaline and acid phases of liver-tissue coincides most closely with that of the diurnal and nocturnal colour-state of the animal.

Thus of eight *M. nigra* diurnes, seven are alkaline as to liver; of five caught at the same time, but exposed on porcelain dishes, until they assumed the nocturnal appearance, all show acid livers. (Table, Tissue Reactions, VII.)

Similarly in *M. flexuosa*, a much more transparent form, an alkaline liver-reaction usually accompanies the diurnal transparent brownish phase; an acid reaction occurs in the transparent colourless or transparent greenish phase. (Table, Tissue Reactions, VIII.) In the former more deeply pigmented form *M. nigra*, a diffuse blue substance makes its appearance during the nocturnal phase, and imparts to the animal the same brilliant colour as that exhibited by nocturnal *Hippolyte varians*. The blue substance in *Macromysis* does not appear gradually exuding from the chromatophore-centres, as is the case with *Hippolyte*, but makes its appearance suddenly throughout the body as though it were produced by some chemical agency acting on a colourless substance distributed generally through the tissues. In some cases, the blueness is

confined to the region of the carapace, as though the agent producing it arose there. A similar partial nocturning is sometimes met with in the middle third only of the body of *Hippolyte varians.*

With respect to the nature of the blue substance of nocturnes, the question naturally arises, "Is it Hæmocyanin"? To answer this question it would be necessary to discuss the prevalent views as to the nature and functions of Hæmocyanin. We propose to leave this discussion for the present and to content ourselves here with recording several facts. In the first place the blue colour of nocturnes (*Macromysis*) is not discharged by carbon dioxide, so that, if the discharge of colour by this gas is a decisive test for Hæmocyanin, we must conclude that the blue substance of *Macromysis* is a different body. In the second place, the blood of *M. nigra*, which is constantly alkaline, exhibits variations of colour. It is colourless in some, and blue in other animals. This blueness we may add in conclusion counts (except in certain green colour-forms) for nothing in diurnal coloration, for then it is masked by the closely woven cloak of diurnal colour.

Though the facts which we have set forth in this section do not warrant a complete or confident hypothesis, we claim that they show :—

1. That the blue substance, to which the characteristic nocturnal colour of *Hippolyte varians* is due, differs physically and physiologically from the red and yellow diurnal pigments.
2. That the nocturnal blue pigment of *Hippolyte*, and a similar diurnal blue substance of *Palæmon*, is produced at the expense of the red and yellow ones ; that it exudes from the chromatophores, permeates the tissues, and subsequently disappears.
3. That its production in *Hippolyte* is contemporaneous with the appearance of acidity in the liver and muscles.
4. That similar phenomena occur in *Macromysis nigra.*

SECTION IX.

The Influence of Light on Littoral Crustacea (*Hippolyte, Macromysis* and *Palæmon*).

Light exerts a potent and varied influence on the littoral Crustacea. Such animals as *Hippolyte, Mysis* and *Palæmon,* instead of becoming inured, remain highly susceptible to the ever-changing light-conditions of their environment. Light plays an important part in controlling not only the movements of these animals, but also the distribution of their pigments. The present section deals mainly with these two modes of reaction to light. But, in addition, light leaves the mark of its influence on the general metabolism and irritability of these animals.

Side by side with an analysis of the modes of response to light, there must be also

an analysis of the light-stimuli themselves. We must determine by virtue of which of its attributes, intensity, colour, or other, light produces its several results. It will be found, however, that it is dangerous to attempt to carry this analysis of light-factors to an absolute conclusion. For often the influence of one factor varies with some other light-factor. For instance, we shall show it is incorrect to describe such an animal as *Macromysis flexuosa* as being positively phototropic, since the direction of its movement, under given conditions of illumination, will change as its background changes.

It is also well to recollect that the responses which light tends to call forth may be inhibited by apparently trivial agents, such, for example, as that of foothold, in the shape of a piece of weed or a rough surface. Light which would cause a roving *Mysis* to fly, may be impotent to make it budge from an anchorage of weed.

We may tabulate thus the various ways in which light affects *Macromysis*, *Palæmon* and *Hippolyte* :—

1. Metabolism and irritability.
2. Orientation and progressive movement.
3. Pigment movement.

1. *The Influence of Light on Metabolism and Irritability.*

A. *Pigment Metabolism.*—Though there is little doubt that pigment arises and persists in the absence of light, yet light certainly plays a part in determining the amount, probably by regulating the decomposition of the pigments of *Hippolyte*, *Macromysis* and *Palæmon.*

We have already given evidence for believing that the chromatophore-centres are centres of active pigmentary changes; that there is a nocturnal exodus of blue substance from the chromatophore-centres of *Hippolyte*; and that this blue substance gradually disappears. We have shown that a similar exudation of blue substance is induced by certain kinds of light-stimuli (white background effect). If the blue substance is a derivative of the red and yellow pigments, and as we have seen there is some evidence that it is, we see in the exuding blue-substance the sign of the influence of light on pigment decomposition. Further, when tracing the development of the colour-patterns, we gave reasons for believing that the final colour-condition of *Hippolyte* is determined by environment. The evidence is all in favour of there being an optimum light-condition under which pigment-production reaches its maximum, and that the more the light-conditions are removed from this optimum the less pigment is produced.

An interesting and instructive pigment condition is not infrequently to be met with among old specimens of *Macromysis nigra.* In these the chromatophore-centres have become gorged with pigment; more has been produced than suffices even to give rise to the blackish coloration of the animal, till, finally, the pressure

of this excess of pigment has become so great as to burst the fine frondose extremities of the branches, and the pigment escapes into the body.

B. *General Metabolism and Irritability.*—Light plays some part in controlling the general metabolism of *Hippolyte, Macromysis* and *Palæmon.* Attention has already been drawn to the periodic formation of an acid-substance by the liver and muscles of *Hippolyte* and *Macromysis.* And it has been shown also that light itself may stimulate the formation of acid-substance in *Macromysis nigra* (acid liver accompanying white background transparent blue phase).

Beside bringing about these changes, light produces an effect on the irritability of the animal. Nightfall is the signal for a striking change in the habits of *Palæmon* and *Hippolyte.* Their day-time tranquillity gives place to a strange restlessness. Animals left over night in shallow dishes, in which they had rested quietly enough during the day, are often found to have flung themselves out during the night. In darkness, the animals swim actively, and a small light in their neighbourhood often causes a violent commotion. As we have mentioned in our earlier paper, heart-beat and scaphognathite-stroke quicken at night. In short, we think that many of the littoral Crustacea, such as *Hippolyte* and *Palæmon,* should be regarded as nocturnal animals. Could we see the littoral fauna at night, it would probably present a busy scene; then, the enforced and purposeful immobility of the day-time is exchanged for a spell of unfettered activity.

2. *The Influence of Light on Orientation and Progressive Movement.*

A. *Orientation.*—Light influences the orientation of the body of various Crustacea such as *Macromysis inermis* and *M. flexuosa*; under certain light-conditions the animals assume peculiar positions. Thus *M. inermis* when placed in a vessel, the background of which is dark, remains in a horizontal or somewhat oblique plane: but if the background is white, it rears itself up vertically and remains for hours motionless "at attention."

Hippolyte varians assumes a similar position when exposed in white porcelain jars. When passing from one background to another, white to black or black to white, *Palæmon* exhibits various flexor movements of the tail, which is bent under and pressed close, crab-wise, against the ventral surface of the body. Amputation of the eye of *Palæmon* also induces a similar attitude.

The whole subject of the light-positions assumed by animals is one worthy of careful investigation. In some cases, such as the latter of the two just mentioned, it appears to be of the nature of shock and purposeless; in others, such as our first example, the light-positions assumed seem to have as much claim to be regarded as purposeful as the progressive movements evoked by light.

B. *Progressive Movement.*—We append a table (Table IX.) summarising our observations on the influence of light on the movements of *Hippolyte, Macromysis*

and *Palæmon.* The two middle columns of the table give the results of experiments made by placing animals in long troughs (about $1\frac{1}{2}$ feet by 6 inches by 3 inches deep), lined with black or white paper. Each trough was provided with a light-proof cover. In one end of the cover, a circular hole was cut and an open cylinder, about 1 foot in height, with blackened sides, was fixed over the opening in the cover, so that light could only enter the trough in a fairly vertical direction. The last column of the table indicates the place taken by animals put in a similar trough, but lined, half with black, half with white paper. It will be seen from the table that the three adults *Palæmon, Macromysis* and *Hippolyte* form a series, of which *Palæmon* is the most light-shunning (negatively phototropic) and *Hippolyte* the most light-seeking (positively phototropic). *Hippolyte* moves up to the light regardless of background, and prefers a white to a black ground, a result altogether surprising to anyone accustomed to search closely for it hiding among weeds.

Macromysis (*M. inermis, M. flexuosa*), on a white ground, moves away from the light: whereas, on a black ground, it moves toward the light.

Even though the light-intensity is lowered very considerably, *Macromysis* still exhibits these movements, now toward, now away from the light, according as the background is light-absorbing or light-scattering. By covering the top of the cylinder through which light is admitted with a black cover, pierced with two or three pinholes, a condition of illumination is reached when background begins to be uncertain in its directive effect; though the average movement of a batch of animals is still in the positive direction with a black ground, and in the negative with a white ground.

When offered a choice of white or black background *Macromysis* selects the black.

The zoeæ of *Hippolyte* show the same reactions as do the adults; but *Palæmon*-zoeæ react in a precisely opposite way to that in which the adults respond to light.

The "choice-reaction" of *Palæmon*-zoeæ (white) is surprising, and decidedly not altogether beneficial, for, as is shown incidentally in Table IX., development proceeds more slowly in light of low intensity, combined with a scattering background, than in an equal intensity combined with an absorbing background.

We were curious to discover whether light could exert an influence powerful enough to cause such a groundling as *Palæmon* to leave the bottom. A bottle containing several specimens of *Palæmon serratus* was covered to within an inch of the bottom with a black cloth. A struggle at once began between disinclination to leave the ground, and desire to avoid the light. In the absence of foothold in the dark region, the former triumphed, and after a perfunctory swim in the shaded part, *Palæmon* dropped down again to the bottom of the bottle. When a stick was placed obliquely in the bottle, *Palæmon* rose, and remained clinging to it in the shadow. These tropisms are of interest in their bearing on the distribution of the adult and larval forms. But, as our experiments show, it is wrong to consider any one of these reactions to light as an inevitable reflex, and therefore also wrong to infer immediately

from the laboratory experiment what will be the movement in the open. The tendency to regard tropisms as simple reflexes, and as inevitably consequent upon a given stimulus, is to be deprecated. To the docility of the pithed frog this tendency is probably due ; but instructive as its reactions are, they are not typical, and the term "reflex" covers a multitude of types of reaction.

The dominating influence of background is further illustrated by the results of experiments made by subjecting *Macromysis flexuosa* to monochromatic lights (red, orange, green, and blue).

When a scattering (white) ground is used in conjunction with monochromatic light the general result is one of movement away from the light; that is, the monochromatic light acts like white light. When an absorbing (black) ground is used in conjunction with monochromatic light, the movement is less certain. Our records show that 33 animals out of 41 (80 per cent.) move towards the illuminated area. That is, in 80 per cent. of cases the reaction is the same as with white light. As to whether special rays are particularly concerned in calling forth these movements, our experiments are inconclusive. Whatever influence special rays may exert, it is overcome by that of "background." With *Hippolyte varians*, also, the direction of movement is the same with monochromatic light as with white light. Red, orange, green, blue, or white light all call forth positively phototropic movements. It scarcely needs to be added that blinded animals cease to respond by their movements to differences in illumination.

The reaction of Crustacea by movement to or from a source of light, and by a choice of rays of different wave-lengths, has been investigated by several naturalists, but we believe that this is the first record of the behaviour of Schizopod and Decapod Crustacea to such forms of stimulation. Earlier observers PAUL BERT (1878), LORD AVEBURY (1881), and GRABER (1884), for example, employed *Daphnia* for this purpose, and their experiments have been repeated by DAVENPORT and CANNON (1897), YERKES (1899), and PARKER (1902) on *Daphnia*, Copepods, and other Entomostraca. The observations of GROOM (1894) and of LOEB (1893) were made on Cirripede larvæ. In the earlier experiments, the *Daphnia* appeared to choose the green rays when a wide spectrum was thrown upon the trough in which they were contained (LORD AVEBURY). GRABER concluded that intensity was the effective light-component, and that the *Daphnia* merely chose a particular optimum intensity.

Later American observers have raised the question whether such Entomostraca do not rather move in the direction of the incident rays than deliberately choose a particular region of light-intensity, and have decided the question in the affirmative. Our observations on the effective agency of "background" raise the whole problem, since it is permissible to doubt that an animal which is phototropic on a white background would be so on a black one. Since we have shown that the reflected as well as the incident light plays a part in deciding the resultant movement, the supposed photopathic response of Entomostraca also requires revision from this point of view.

3. *The Influence of Light on Pigment Movement.*

A. Mode of recording pigment movements.
B. Periodicity : a possible source of error in interpreting records.
C. The chief colour-phases induced by various light-conditions.
D. The factors in pigment-movements :—

Intensity.
Background.
Monochromatic light.

E. Conclusions and critical considerations.

A. *Mode of recording Pigment Movements.*—At first sight there may not appear to be any particular difficulty in making satisfactory records of the results of experiments in pigment-movements. Difficulties, however, soon present themselves. All records must be made under fairly comparable light-conditions. Therefore animals, the state of whose pigments are to be observed, must be brought from the light to which they were subjected during experiment into such light as is selected for the purpose of recording results. But this exposes them to a change of light-stimulation. Moreover, the better the light is by which the animals are viewed, the greater is the danger of its producing a disturbing effect. Rapidity of examination, obtained by practice and the co-operation of two workers, minimises this danger ; and a knowledge of the effect which the standard light tends to produce, enables us to discount its disturbing influence.

But other and more serious difficulties remain.

First, naked-eye estimation of the gross colour is not a sufficient mode of recording pigment movements. An animal may give the impression of transparency, though the pigments are not absolutely contracted.

Second, a microscopic examination, by means of which small degrees of expansion are observed, tends to emphasise unduly this expansion. Therefore it is necessary to combine naked-eye with microscopic records.

Third, the pigments of *Hippolyte*, *Macromysis* and *Palæmon* fall into two series. One series, including red and yellow, produces its optical effects by transmitting light. In tables of records we refer to these as the transmitting (T) pigments. The other series, frosted white, frosted yellow and blue, only give rise to these colour-effects when viewed by reflected lights—reflecting (R) pigments. Hence microscopic records must be made by transmitted and by reflected light.

Fourth, the different pigments of either group contract or expand at different rates, and so the conditions of the individual pigments must be recorded.

Fifth, though it is true that the chromatophore-system is to be regarded as a whole, whose constituent parts act, broadly speaking, in unison, yet the various

groups of chromatophores (neural, visceral, and caudal) may have, every one, a different rate of reaction to a given light-stimulus. Thus, as a result of stimulation, the dorsal and ventral surfaces of an animal may present unlike conditions of pigmentation, *cf.* Table XIII.; nay, more, distinct degrees of expansion or contraction may be exhibited by the various chromatophores of any one group.

Any record must therefore be of the nature of a compromise, or of an estimate based on naked-eye observation and on microscopic examination, and by transmitted and reflected light. Large numbers of animals must be experimented upon, and those selected for examination must be typical, and must be rejected after having served as samples. The statement of the naked-eye record must be bold and precise, that of the microscopic record precise and minute. Even after practice has produced a considerable degree of expertness, certain pigment-states will always baffle description, and many records have to be abandoned because their descriptions, seemingly adequate at the time, prove to be inefficient to call up a mental picture of the pigment-states which they purport to describe.

B. *Periodicity: a Possible Source of Error in Interpreting Records.*

In interpreting the results of any experiment on the influence of a given light-stimulus on pigment-movement, the phenomenon of periodicity must be borne in mind. As we point out, at the conclusion of this section, POUCHET denied the existence of any periodic light-movement in these animals.

We have already shown (1900) that the regular alternation of day and night sets up a rhythmic expansion and contraction of the pigments of *Hippolyte varians.*

We now know that this diurnal flood and nocturnal ebb of pigment is characteristic also of *Macromysis*, *e.g.*, *M. inermis*, *M. flexuosa*, and of the just hatched zoeæ of *Palæmon.* As the case of *Palæmon* seems to us particularly interesting, we give in tabular form in the Appendix the results of an experiment in which this conclusion is based (Table X.). About seventy-two zoeæ of *Palæmon squilla,* hatched out on August 23, 1901, and, on the following day (24th), were put and maintained in the dark, except for intervals of about 1 minute, when they were exposed to light for observation. The table shows that some expansion occurred on the 24th, followed by complete contraction in the evening of that day, renewed expansion on the morning of the 25th, and contraction once again in the evening. After the third morning the pigments of the animals passed into a permanently contracted condition. On the 27th the zoeæ were active, and had developed to the stalk-eye stage; on the 28th they died.

It would be interesting to consider how this pigment-rhythm comes to be a property of so young an animal; to ask whether it is acquired with extraordinary rapidity in response to external conditions, or whether it is an expression of alternating nervous states not originally called forth by environment.

We do not propose, however, to enter into a thorough discussion of the phenomenon of periodicity; but to consider more particularly the disturbing effect of periodicity on the results of any given stimulus. The nature of this effect may be readily imagined, and the effect itself not infrequently makes itself felt. One example must suffice. Under certain conditions of illumination, pigment contraction takes place. The experiment runs on, night falls, contraction persists. In the morning a temporary expansion occurs, which soon gives place to a re-contraction. It is generally easy to allow for complications of this sort by performing experiments at various times of the day, and by comparing the results; but negative results become very troublesome; an element of uncertainty attaches, for example, to many of our experiments on the effect of monochromatic light, owing to the fact that failure to produce a pigment movement does not necessarily mean failure to effect a stimulation of that pigment.

C. *The Chief Colour-phases induced by various Light-conditions.*

Certain conditions of illumination call forth definite pigment movements, which result in the production of well-marked colour-phases in *Hippolyte*, *Macromysis*, and *Palæmon*. These we now describe, not only on account of their intrinsic interest, but also because they serve as useful starting-points for further experiment. In the case of *Palæmon*, they have been previously described by POUCHET (1876).

1. *Dark* (*Contracted*) *Phase.*—In darkness, the pigments of *Hippolyte*, *Macromysis*, or *Palæmon*, become completely contracted into their chromatophore-centres. These centres now appear as minute dots, so widely separated as not to interfere with the general transparency of the body.

The rapidity with which this transparent phase may be assumed varies very considerably, both with the time of day and with the condition of the animal. At times, ten or a less number of minutes suffices (*Hippolyte*), at other times an hour or even two is required.

In *Hippolyte* and also in some species of *Macromysis*, this phase is accompanied by the appearance of a diffuse blue substance (nocturnal coloration). The blue substance, giving rise to the nocturnal colour, is derived, in *Hippolyte*, from the chromatophores themselves whence it suffuses, spreading throughout the tissues.

2. *White background* (*contracted*) *phase.*—The term "white background phase" is very open to objection, but convenience prescribes it. We use it to denote the transparent condition (combined with diffuse blueness in *Hippolyte* and certain Mysidæ) which is induced by exposure of the animals to light in white, porcelain, or paper-covered vessels. In this phase, as in the last, the pigments are fully contracted. It may be and generally is assumed with great rapidity: less than a minute often sufficing to call it forth in *Hippolyte* or *Macromysis flexuosa.*

One of the most convenient forms in which to follow these pigment movements is *Macromysis inermis*. In this animal, the light-transmitting (T-series) of pigments are the first to contract under the influence of the scattered light; later the less-expanded reflecting pigments (R-series) contract, and so complete transparency is produced.

Palæmon, which is, from the point of view of colour-physiology, a complete but poorly working *Hippolyte*, displays a temporary blue phase when first placed on a white ground. But the blue substance exuded from the chromatophore-centres is only sufficient to form pale halos about them and soon disappears.

3. *Mid-phase.*—Freshly caught *Macromysis* (*M. inermis, M. flexuosa*) generally have their pigments moderately expanded. A similar condition is presented by animals confined in glass tanks or bottles, and as a starting-point for experiment this phase is less useful than the others. A similar mid-condition is found in *Palæmon* under similar circumstances. But it does not seem to occur in *Hippolyte*. Here the pigments during the day are either fully expanded and, if induced by darkness or other change of light-condition to contract, they contract completely.

4. *Dark-background* (*expanded*) *phase.*—The pigments of *Macromysis* and of *Palæmon* expand rapidly when these animals are placed in black-bottomed vessels. The close networks of chromatophore-branches, becoming injected with pigments, give rise to the dark colours which characterise animals on a dark background.

Thus, in this phase, *M. nigra* has an almost black, and *Palæmon serratus*, a speckled yellow, orange, or brown colour; the speckled appearance being due to the separation of the branches of one chromatophore from those of others by transparent areas.

These various colour-phases persist for a long time; are indeed permanent as long as the light-conditions remain unchanged or till periodicity sets up a contraction or an expansion. At nightfall, the pigments, expanded in the dark background phase, contract, but that phase is resumed on the morrow.

D. *Factors in Pigment Movement.*

Light-intensity.—We have now to consider more closely the various phases of pigment movement in order to determine, if possible, what part light-intensity plays in determining these movements. When we watch the gradual contraction of the diurnal pigments of *Hippolytes* during the fading evening light, no doubt arises in our minds of the efficiency of change in light-intensity as a stimulus to pigment-movement. But when we turn to *Palæmon* or *Macromysis* and observe that the white background, contracted phase or the dark background, expanded phase is produced no matter whether the light-intensity is low or high, constant or variable, we are compelled to recognise that something beside intensity is at work. With that something we deal immediately, but first attempt to decide to what extent light-

intensity may modify pigment movement. The following observations will help us to a conclusion :—

Hippolyte, whose eyes are removed, may suddenly become transparent; their pigments retract and the nocturnal phase is induced.

If, after amputation of the eyes, *Macromysis* or *Palæmon* is placed in a white porcelain vessel, their pigments, instead of assuming the contracted condition, become fully expanded. Indeed, in the case of *Palæmon*, a deep chocolate colour is produced, far darker and richer than is ever to be seen even in the expanded dark-background phase. Under these conditions the pigments go on expanding to the very utmost.

In darkness, as we have previously shown, contraction of the pigments of eye-amputated *Hippolyte* takes place; showing that the mechanism for expansion and contraction is still intact, although the chief means of putting that mechanism in motion—the eye and its nervous connections—is no longer operative.

Again, the isolated chromatophores of *Palæmon* or *Hippolyte*, or to speak more properly, the chromatophores in a piece of skin of either of these animals—are sensitive to light. When examined microscopically in a bright light the pigments are seen to expand.

We conclude that the chromatophores are directly sensitive to light, but that in practice their direct reaction is checked or annulled by the eye, acting through the nervous system. Thus, the porcelain effect on the chromatophores themselves is to produce expansion; and is simply a response on the part of the chromatophores to a high light-intensity. In intact animals, this direct effect fails to be produced or at all events to be maintained. It is inhibited by impulses proceeding from the eye. Even in the expanded phase, these inhibitive impulses are not altogether lacking, since, as we have seen with *Palæmon*, the pigments are capable of greater expansion (in blinded animals) than characterises even the black-background, expanded phase. In the dark, all stimulation, both direct and indirect, ceases, and full contraction occurs. We are now in a position to interpret a very puzzling reaction which is exhibited by *Macromysis inermis* when taken from darkness (dark contracted phase) and put on a white porcelain ground. Under these circumstances, there is a temporary expansion of pigment, succeeded by the normal, white-background, contracted phase. The temporary expansion is to be regarded as a direct response to light-intensity comparable to that manifested by an isolated chromatophore or by a blinded animal in a porcelain background. Taken from darkness to scattered white light, the eye-mechanism is temporarily thrown out of gear, or rather is pre-occupied for the moment. It has its own business to attend to, that of redistributing its retinal pigment in response to the new light-conditions. The chromatophore is free for a time to respond, by pigment-movement, to the stimulus of light-intensity. Soon, however, the eye-mechanism resumes control—as we think, automatically with the adjustment of its retinal pigment—and promptly vetos this independent activity of the chromatophore.

As far as this independent action is concerned, the nature of the background (white or black) counts for nothing; intensity provides the stimulus. It is otherwise, as we shall see, with the response called forth through the mediation of the eye.

The pigments of the chromatophores, then, react directly to changes in light-intensity, expanding in obedience to a higher and contracting in obedience to a lower light-intensity.

But generally, in the intact adult animal, these responses are masked or reversed by the more permanent and more purposeful, indirect reaction induced by the eye and nervous system.

Examples of the direct reaction to intensity in the intact animal are: the transitory expansion in porcelain and the contraction with failing light (though here other factors co-operate); in the blind animal, the permanent expansion on porcelain; in the isolated chromatophores, its expansion in response to raised light-intensity; and, in larval *Hippolyte* and *Palæmon*, their expansion of pigment on white and on black grounds. (Tables XIII. and XIV.)

In the natural distribution of pigment in *Mysis* and *Palæmon*, intensity counts for little. We must look elsewhere for the light-factor which modifies the actual pattern of the animal in its free state.

Background.—In 1898 we were engaged in investigating the nocturnal (transparent blue) phase of *Hippolyte*. Since, in this phase, the pigments are fully contracted, it serves as a very convenient starting point for experimentation. We hoped thus to determine whether special rays of light were specially responsible for producing expansion of the pigments. The results of our experiments with monochromatic light were altogether variable. This uncertainty we found to be due to our neglect to preserve uniformity in the vessels used. In order to insure a high light-intensity we whitened the jars in which the animals were contained. The result was that our nocturnes refused to recover to their diurnal state and we were obliged to recognise the importance of the influence of background. To this influence POUCHET has already drawn attention, as we have indicated in the introduction, but as he expressly states, his treatment of this factor is quite simple.

Our experiments show that this factor transcends all others in importance.

In illustration of this, and to show how, compared with this influence of backgrounds, that of light-intensity is of small importance, we mention the following experiment, which we have often performed with *Hippolyte* and with *Macromysis.* We take with us on a collecting expedition four jars, two of glass wrapped round with black cloth, and two of porcelain. For one of the former pair and one of the latter we provide covers of white or black paper pierced with several pinholes. As the animals are caught they are distributed between the four jars. When brought into the laboratory and examined, the animals in "open" porcelain and in "pinhole" porcelain are found to be in the fully contracted phase; those in the "open black" and "pinhole" black jars are in the fully expanded black background phase. Now

the light-intensity in the open jars is far higher than that to which the animals were subjected before capture, and the intensity in the pinhole jars is probably far lower. Any effect which a raised or lowered light-intensity might produce is swamped by the background effect. The latter is of such a nature that an absorbing (black) background induces expansion, and a scattering (white) background produces complete contraction, and these effects are produced even in the faintest (pinhole) light.

A comparison between the pigment-movements induced by a scattering (white) background and those called forth by a reflecting (mirror) background gives a striking result In the former case, the pigments become fully contracted; in the latter, they pass to a mid-condition. Both sets are subjected to an equally high (or low) direct illumination and yet, owing to the differences of the background, the results differ greatly.

That it is, in some way or other, the ratio $\frac{\text{direct}}{\text{scattered}}$ light which determines the porcelain, contracted phase is certain; for if animals are kept in scattered light, for example, if the porcelain jar containing them is covered with beeswaxed paper, the mid-phase is induced.

From the evidence given already, we know that the reaction to white background is determined by the eye and nervous system. Therefore we must search for the meaning of the reaction in the eye itself. In some way, the eye differentiates between the direct and the irregularly scattered light, in other words, it displays a certain dorsi-ventrality. To establish fully the nature of this dorsi-ventrality both histological and physiological investigations are necessary. We have as yet pursued only the physiological line of inquiry. By it we are able to show that the dorsi-ventrality is probably not due to a permanent structural difference in the two sides of the eye.

If the animal, *e.g.*, *Macromysis inermis*, is inverted as it were, by inverting the light conditions, the reactions to background still take place; animals, placed in glass vessels, covered top and sides with black cloth and illuminated from below, pass into the black-background expanded phase. If the top and sides of the glass vessel are covered with white paper, illumination from below produces the white-background contracted effect. (Table XVI., inverted backgrounds.) We infer, therefore, that the dorsi-ventrality is produced by some mobile structure which takes up its position in response to the light-conditions, and whose position determines the nature of the stimulus imparted to the nervous element of the eye. The retinal pigment is such a mobile substance. It is known to be photo-sensitive, and we suggest that histological investigation will show that, during these exposures to various backgrounds, the distribution of the retinal pigments is so modified that the retinal elements are screened in varying degrees. We do not attempt to carry our hypothesis further, although it would not be difficult to draw a rude picture of how this might produce the known results. We hope to attempt, on an early occasion, the verification, or disproving, of our hypothesis by means of histological investigation.

It is natural to suppose that reaction to background is of the nature of an adaptation to a littoral habitat and, indeed, experiments with larval *Hippolyte* and *Palæmon* lend support to the view, as will be seen from the first line of Table XI. The pigments of *Hippolyte*-zoeæ react at all events with less certainty to background than do those of adult *Hippolyte* (Table XII.). Such is also the case with the zoeæ of *Palæmon*. When removed from darkness to light the pigments expand, whether the background is black or white; but, as Table XIV. shows, an appreciable amount of difference may be noticed after some time between the conditions of pigment in zoeæ in "porcelain pinhole-cover" vessels and in "black-background pinhole-cover" vessels. It is to be noted that in the course of this experiment the stalk-eye stage was reached and the slight reaction appeared about this stage. The result is one which we should expect from what we know of the part played by the eye in determining background reaction. We conclude that "background" reactions only come into prominence when the eyes have become well developed, and that perhaps this late appearance may be taken to indicate an adaptation to environment.

As we show in another section (Section V., p. 328), the background effects on pigment-movements, help us to imagine how light modifies pigment-development, and thus causes such an animal as *Hippolyte* to "grow into" its surroundings, modelling its diurnal pigment-distribution on the distribution of light and shade on its background.

The indirect background-reaction, dominating as it does the direct intensity-reaction of the chromatophore-pigments, enables us also to understand how, in spite of the ever varying light-conditions of the environment, *Hippolyte* is enabled to hold fast to its colour-pattern. As long as its background is unchanged, change of intensity avails little. Now of all things which characterise *Hippolyte*, its tenacious immobility on the weed of its choice is the most striking.

As Table XIV. shows, the nature of the background upon which hatching experiments are carried out, may not be without importance; in that case, at all events, the stalk-eye stage of *Palæmon* was reached a day sooner in dim light on a dark background than in similar light on a white background. It is not improbable that it would be worth the while of those face to face with the strange difficulties of hatching, to learn as much as possible of the light-reactions and light-requirements of the animals in whose rearing they are interested.

We may summarise our chief conclusions thus :—

(1) Changes of light-intensity may produce changes in pigment-distribution.

(2) The stimulus of change of intensity acts directly on the chromatophores.

(3) In contrast with the direct and transient stimulus of light-intensity, that of background is indirect and enduring.

(4) Nevertheless the measure, small though it seems, of local control is probably of importance; by taking it into account we are enabled to realise how the complex pattern of an *Hippolyte* is arrived at. (Section V., pp. 327–328.)

(5) There is some evidence to show that background influences pigment movement by first setting up changes in retinal pigments.
(6) Differences of background (black and white) give rise to greater differences in pigment distribution than do great changes in light-intensity; indeed the effect of backgrounds are comparable to those produced by light and darkness.

Of these conclusions (3) was already reached by POUCHET (1876). The explanation that we offer of this background result and of the action of light-intensity are, we believe, made for the first time.

Monochromatic Light (*Red, Orange, Green and Blue*).

In our experiments on the influence of coloured light on pigment movements we use colour-screens of various kinds; in some experiments we employ, exclusively, colour filters consisting of the fluids recommended by LANDOLT; in others we use, for red, red glass and for green, combinations of gelatine films supplied by BAKER (London), and by ZIMMERMANN (Leipzig).

The vessels for the liquid screens we make as follows. Stout indiarubber rings (washers) of the requisite height are procured; a small circular hole, which may be closed with a cork, is stamped by the maker in the side of each ring. A ring is affixed to a glass plate by indiarubber solution, and then a glass cover is similarly fixed over the ring and held in place till the indiarubber solution is set. A second ring is fixed on the top of this cover and is itself covered with another glass plate, which, like the others, is affixed by indiarubber solution. Thus a fairly cheap, large, two-celled vessel is obtained. The proper fluids are introduced through the holes in the sides of the rings; each cell is completely filled, covered and the cork sealed. Such a cell will last for a very long time; with certain solutions, for years.

Unfortunately in one of LANDOLT's colour-filters, permanganate of potash is required and this cannot be used with the indiarubber. Gelatine films, well sealed up, last for some time, but must be always tested spectroscopically before being employed. We must confess that we are far from satisfied with our "colour-filters," but have been compelled to use them in default of a better means of obtaining monochromatic light. The rays transmitted by them are given on p. 378.

The ultimate effect of monochromatic light (red, orange, green and blue) on pigment-movement is a surprising one; at all events it is surprising before the influence of background combined with white light is fully appreciated. The main result of exposing *Macromysis*, *Palæmon* or *Hippolyte* to monochromatic light is determined, not by the nature of the light, but by the background. Red, orange, green and blue light produce a contraction when the background is of white; an expansion of pigment when the background is black; in other words the final result is the same with monochromatic as with white light, and, in all, the background

determines the result. This is shown in a striking manner when the results of a large number of experiments on *Macromysis inermis* are expressed in the form of a target. (see Target Diagram, p. 377). In this diagram every animal whose chromatophores showed contraction as the result of a monochromatic light-stimulus, is represented by a dot in the "bull" of the target; and every animal whose chromatophores expanded under the stimulus is represented by a dot in the outermost circle of the target; intermediate results are scored in the two middle rings of the target. The only reason for having two middle rings is to increase the chances of accuracy in estimating any intermediate results. In reading the scores, the inner-mids might be counted with the "bulls" and the outer-mids with the "magpies."

The shaded half of the diagram contains the results of the action of monochromatic lights (red, orange, green and blue), on *Macromysis inermis* on an absorbing (black) background; the unshaded half, those of the action of the same monochromatic lights on a scattering (white) background. A glance at the target diagram suffices to reveal the dominating influence of background. On the shaded half, expansion is the general rule, on the unshaded half, contraction.

The statistical table accompanying the target shows that on the white scattering ground, 78 per cent. of the animals have their pigments, as a result of the stimulation, in a fully or fairly contracted condition; 21 per cent. in a fairly or fully expanded state; whilst on the absorbing background the numbers are reversed, 21 per cent. full or fair contraction, 78 per cent. full or fair expansion.

The above results were obtained at Cullercoats (Northumberland) in 1900. Yet more definite results are shown by an analysis of experiments made at Roscoff in 1901:—

$$\text{On a white ground}\begin{cases}\text{89 per cent. full or fair contraction.}\\\text{11 per cent. fair or full expansion.}\end{cases}$$

$$\text{On a black ground}\begin{cases}\text{8 per cent. full or fair contraction.}\\\text{92 per cent. fair or full expansion.}\end{cases}$$

The overwhelming influence of background in determining pigment-movement is true not only in the case of *Macromysis inermis* and other species but also in that of *Palæmon.*

Table XV. records the changes induced in the pigments of *Palæmon squilla* by exposure of the animal to white or monochromatic light now on a white, now on a black background.

The red and yellow pigments both react to background, expanding on a black, and contracting on a white, ground; and also as in *Hippolyte*, a blue diffuse substance exudes from the chromatophore-centres when *Palæmons* are placed on a scattering background, endures for a time and finally disappears.

Again, as in *Hippolyte*, the yellow pigment not present in the Mysids, reacts more rapidly than the red.

As the facts abundantly show, *Palæmon* is, from a colour point of view, practically identical with *Hippolyte*; it contains pigments of similar colours; these pigments react similarly to light.

But, to return from the contrast, to the agreement, between these two forms: we find, in the reactions of *Palæmon* to white and monochromatic lights combined with white or with black backgrounds, the same reaction to background which also characterises both *Hippolyte* and *Macromysis.* The reaction appears to be general among the littoral crustacea. As with white light, so with monochromatic light, inversion of the light-conditions of the animal, putting, for instance, the "background" above and illuminating from below, produces the same effect as normal illumination. As Table XVI. (Inverted Backgrounds) shows for *Macromysis* and for *Palæmon,* when the background is white (scattering), contraction occurs; when black, expansion; when a mirror (reflecting), a mid condition of partial expansion is assumed by the pigments.

The time required for monochromatic light in conjunction with background to produce their redistributions in the pigments of *Macromysis inermis* varies considerably. In these experiments, the stimulus acts slowly, commencing to produce an effect within a few minutes, but not acting fully for an hour or more.

These results, showing the influence of background in determining reactions to monochromatic light, help us to understand why, in our earlier experiments already referred to, on the influence of monochromatic light in inducing recovery of nocturnal *Hippolyte,* we failed to get decisive results. These *Hippolyte*-experiments, when tabulated according to the background used, prove conclusively that *Hippolyte* reacts to background just as does *Macromysis.* Monochromatic light (red, orange, green and blue) in conjunction with a scattering white background tends to maintain the nocturnal phase; the same lights, on a black ground, induce recovery therefrom. From a very large number of records, of which those given in the target diagram are samples, we are unable to draw any certain conclusions as to a specific colour effect of monochromatic light in the pigment movements of *Macromysis inermis.* At times one colour, at times another, produces its effect more rapidly. Hence the probability is that these differences of rate are due to differences in the conditions of the animals used and not due to a special sensibility to any particular colour. Nor should we expect, under the conditions of these experiments, to discover any specific colour effect even though such exists; for on the white and black grounds the animal, as we have seen in the case of white light, appeals for pigment-guidance to the amount of light *scattered* or *absorbed* from the ground; or, as we put it previously, it is a reaction to the ratio $\frac{\text{direct}}{\text{reflected}}$ light. We conclude that the eye of *Macromysis inermis* has no appreciation of colour as such. Any effect produced on the chromatophores through the mediation of the eye is an effect of background.

Nevertheless, we have amassed a large number of results which show that light of

a certain colour does exert a specific influence on the chromatophores of *Macromysis inermis*. Just as animals brought from darkness and exposed to white light in a white porcelain vessel exhibit a temporary expansion before settling down to the porcelain contracted phase, so when green light is employed, in conjunction with a white porcelain ground, a similar transient expansion is induced.

Again, when animals in the black-background, expanded phase are maintained on that ground but subjected to green light, a temporary contraction of pigment often takes place. Yet, again, a transient expansion is often produced in animals in the contracted white-background phase by covering the containing vessel with a green screen. These reactions are produced very frequently by green light, very occasionally by orange, and very rarely indeed by red or blue. We regard them as indicating, like the similar temporary reaction to white light, a direct response on the part of the chromatophore to the *direct* light.

It is noteworthy that in the first-mentioned responses of *Macromysis inermis* to green light, the *mode* of reaction depends on the previous condition of the chromatophore pigments. If, previous to the stimulus, they were expanded, they contract; if contracted, they expand. We may liken such reactions to the sudden start or sudden stop called forth in ourselves by a flash of light; as, for example, when the electric light is switched on unexpectedly. As the sudden movement gives place to a steady attention, so the sudden contraction or expansion gives place to the steady background reaction. The one is "shock" and purposeless, the other is purposeful.

Before summarising our conclusions we wish to point out that, in all experiments on phototropism, the possible influence of background must be taken into consideration. Whether it is a late adaptation to peculiarity of habitat or not, it is certainly of general occurrence. We hope ourselves to investigate it especially with a view of determining whether it makes itself felt among the lower animals. In the meanwhile we suggest that neglect to take note of the background used in any experiment into the influence of light on a given animal, is liable to vitiate results.

E. Discussion of Results in Reference to Work by Pouchet and Professor Poulton on "Backgrounds."

We will conclude this section first, by pointing out how far our conclusions confirm those arrived at by Pouchet, and where they differ from his; and second, by drawing attention to the parallel presented by the results of these observations on the influence of light on the movement of pigment in the Crustacea, and the results of Professor Poulton's researches on the influence of light on the formation of pigment in lepidopterous larvæ and pupæ (1887, 1893).

Pouchet's main conclusion that the chief light-factor in producing pigment movements is background, is fully confirmed by our experiments. What Pouchet showed was the case when broad daylight and white or black backgrounds only were

used, we show to be also true, when white light of variable intensity and monochromatic light (red, orange, green or blue) are employed in combination with scattering (white) or absorbing (black) backgrounds. POUCHET proved that these enduring and, in large measure purposeful, reactions are produced indirectly through the mediation of the eye and nervous system, but he failed to observe that in addition to these reactions, a light-stimulus may, by acting directly on the chromatophores, also call forth an immediate and transitory response.

POUCHET denied to Crustacea what he in some measure recognised as belonging to fish, the power to exhibit a prolonged after-effect of stimulation. Thus he states that alternation of night and day produces no change in colour-state. This we have shown to be an error. Nocturnal and diurnal movements occur, and the phase of the rhythm in which the animal finds itself, may prevent a light-stimulus from taking effect at one moment, whilst facilitating it at another.

POUCHET left the mode of action of the background upon the eye unexplained and the problems of pigment-formation and chromatophore-development untouched. We have attempted to fill these gaps, and as a first step thereto, we give the results of our observations on inverted backgrounds, and on the inheritance of the colour-systems of various Crustacea, and on the influence which environment exerts in the case of *Hippolyte varians* in modifying the system which inheritance brings forth.

The results obtained with respect to background as the chief factor in inducing pigment *movement* in Crustacea offer a curious and interesting parallel to the results of Professor POULTON on the *formation* of pigment in lepidopterous larvæ and pupæ. Professor POULTON has shown that in susceptible larvæ, white backgrounds inhibit the formation of pigment, whilst black backgrounds favour this formation. This result holds, whether the incident light is strong or feeble, and whether it is white or monochromatic (red, orange, yellow or green). If we replace the word "formation" by the word "movement," the foregoing conclusion summarises the state of affairs in Crustacea. Certain differences between pigment-formation in susceptible larvæ, and pigment-movement in Crustacea, occur: for example, blue light on a white ground tends to produce pigments in such larvæ, but to contract pigments in Crustacea. Nevertheless the apparent identity of the external influences which regulate the two processes, deserves emphasis.

F. *Conclusions.*

1. Light exerts an influence on metabolism, growth and irritability. It also calls forth orientations; movements of the whole animal; and of the pigments of its chromatophore-system.

2. The influence of light should be taken into account in all hatching operations (see observations on the development of the zoea of *Palæmon*, p. 355).

3. Some orientations appear to be due to shock and are transient and "purpose-

less"; others are enduring and as "purposeful" as the movements of progression induced by light.

4. The movements of the animal in response to light are brought about through the mediation of the eye and nervous system.

5. The light-factor most powerful in producing movements is "*background*."

6. The reaction of *Macromysis inermis* to a given light is determined, as to direction, by background. On a white ground it is positively phototropic, on a black ground, negatively phototropic.

7. The reaction to background manifests itself through a wide range of light-intensity.

8. On a given background, the direction of the light-induced movement in *Hippolyte*-zoeæ is the same as that of the adult, but in *Palæmon* the zoeæ move in the opposite direction to the adults; on a white ground, the adult is negatively, the larva, positively phototropic.

9. *Hippolyte*, *Macromysis* and *Palæmon*, all exhibit a marked "choice" of background; *Hippolyte* choosing white, the others black. *Hippolyte*-zoeæ, like the adults, choose white; *Palæmon*-zoeæ, unlike the adults, choose white.

10. The kind of choice made could not always (*e.g.*, with *Hippolyte*) be predicted from a knowledge of the habits of the animal.

11. Light also induces vertical movements (*Palæmon*).

Pigment Movements.

12. Light calls forth movements of the pigments of the chromatophores of *Hippolyte*, *Macromysis* and *Palæmon*.

These reactions are of a twofold nature; in part a direct response, and in part an indirect response in which eye and nervous system play a part.

13. As far as colour-display is concerned, the indirect response is the more important.

14. In the adult, the direct response is comparatively sudden, transitory and, from the point of view of protection, purposeless. It is soon dominated by the indirect response, which is comparatively slow, enduring and purposeful.

15. The *direct* response of the chromatophore-pigments is not determined by background, but by the incident light.

16. The *indirect* response (contraction or expansion) is determined by background. A white ground causes contraction of pigments through a wide range of intensity, a black ground expansion, in like manner.

17. Scattered light (light from a white porcelain ground) produces much more contraction than reflected light of equal intensity.

18. A reversal of the light-conditions, *e.g.*, illumination from below, the top and sides of the vessel being covered with white or black material, produces the normal

white or black-background effect. Hence the conclusion that the eye-mechanism, which interprets the *way in which light falls*, is a mobile one; the background effect in the chromatophore-pigment is probably a consequence of a light-induced, asymmetrical distribution of retinal pigment.

19. There is a close agreement between the phototropic reaction and the pigment-movement reaction; both depend on the eye and both are determined by "background."

20. A monochromatic light in conjunction with a scattering (white) or absorbing (black) background, produces the same ultimate effect on pigment-movement as does a white light in conjunction with the same background.

21. A specific effect of monochromatic light is hard to demonstrate, but the evidence favours the view that *green* light exerts a specific effect, and that this effect is due to a *direct* response of the chromatophore, and is not brought about through the eye and nervous system.

22. The reaction to green light is like the direct reaction of the chromatophore to incident light, rapid, transient and "purposeless."

23. Larval *Hippolyte* (zoeæ) do not show the background reaction: *Palæmon*-zoeæ show it poorly. The background reactions may be a special adaptation to a littoral habitat, but we reserve our opinion. It is certainly very general.

24. The factor of background must be taken into consideration in all experiments on phototropism.

SECTION X.

General Summary.

We bring together here the chief conclusions to which our work has led us. A fuller statement of these conclusions is to be found in the summaries appended to the several sections of this paper.

A. *The Influence of Light.*

1. Under the influence of light the secretory activity of certain organs is modified, an acid-substance appears periodically in the liver and muscle: the appearance and disappearance of acid-substance in liver and muscle coincides broadly with nocturnal and diurnal colour-change.

2. In the progressive movements and orientations called forth by light, *background is the most powerful factor*, more powerful than change of light-intensity. By change of background, black to white, the direction of a light-induced movement may be reversed. This directive effect of light was not recognised by Pouchet.

3. The response of the chromatophore-pigments to light is of a twofold nature: direct, and indirect through the mediation of the eye. The indirect response alone

leads to an enduring redistribution of pigment. The direct response is a reaction to light intensity. The indirect response is through a wide range, independent of variations of intensity. POUCHET's discovery of the effect of background is thus carried a step further.

4. The ultimate effect of monochromatic light on pigment-movement is the same as that of white light; as with the latter, so with monochromatic light, background-white (scattering), black (absorbing), mirror (reflecting)—determines the nature and extent of the pigment movements. In describing an effect of light, that light must be considered in combination with its background. Neglect to do this must lead to erroneous conclusions.

5. "Reaction to background" is traceable to the eye and is probably a consequence of an asymmetrical redistribution of retinal pigment, brought about not by changes in the amount of light falling on the eye, so much as by changes in the way in which light falls on the eye.

B. *The Rôle of Pigments.*

6. The phenomena presented by the pigments are not exhaustively explained by any "protective" hypothesis.

A nocturnal translocation of a blue substance, produced, as there is evidence for believing, at the expense of the chromatophore-pigments, takes place. The blue substance passes from the chromatophore-centres, persists for a time in the body, and ultimately disappears.

C. *Morphology.*

7. The chromatophore-system of Mysidæ is built upon a common plan, of which the genera and species present, severally, a constant modification. This we call the *primary* chromatophore-system.

8. Decapods possess a *primary* and a *secondary* system of chromatophores. The primary system appears in the embryo, is completed in the "Mysis-stage," persists throughout life, but takes no part in the ultimate colour-pattern.

The secondary system arises in an early stage of development, increases in extent throughout life, and to it the colour-patterns of adolescent and adult are due.

9. The chromatophores of the primary system are profusely branched, few in numbers, segmentally arranged and centralised; those of the secondary system are sparsely branched, numerous, irregularly arranged and decentralised.

D. *Histology.*

10. The chromatophores of Mysidæ are multicellular organs. Those of the neural group are developed from the epidermis; losing connection with the epidermis, they acquire a close relation with the central nervous system: indeed the distribution

of the chromatophores of the primary system follows that of the ganglionic parts of the nervous system.

11. The chromatophores of Decapods are plurinuclear structures, their distribution is not confined to the ganglionic parts of the nervous system.

E. *Taxonomy.*

12. The primary systems afford assistance in the determination of genera and species. By their aid, animals, in early as well as in late stages of development, may be diagnosed.

F. *Inheritance.*

13. The primary chromatophore-systems of the Mysidæ are completely outlined in the embryo. The development and constancy of these primary systems is strong evidence of their inherited character.

14. The adult colour-pattern of *Palæmon* and of *Crangon* are constant and develop directly. The evidence tends to prove that both secondary and primary chromatophore-systems are inherited.

15. The adult colour-pattern of *Hippolyte cranchii* is constant, but develops indirectly. The adolescent animal possesses a special colour-pattern, developed in large measure, in relation with the primary system of the zoea. Both persist, though concealed by the adult pattern which arises independently.

16. In *Hippolyte varians* several adult colour-patterns occur. They develop indirectly. The primary system is the same in all.

In the adolescent, three distinct colour-patterns arise, viz., "barred," "lined," "monochrome." These may persist, becoming barred, lined or monochrome adult.

Or, either barred- or lined-form may, by developing superficial or deep chromatophores, become a monochrome.

Or, by localised superficial developments, either barred or lined, may give rise to a blotched adult form, under which the adolescent pattern is hidden.

Primary system inherited; adolescent colour patterns possibly inherited, but inheritance immaterial since final goal reached by any adolescent road; that is, adult colour-pattern the result of environment.

TABLE I.—To illustrate the Arrangement of the Primary System of Chromatophores in certain Mysidæ.

	Segment.	*Macromysis*			*Schistomysis*					*Leptomysis*		*Mysidopsis*		*Macropsis slabberi.*	*Siriella armata.*
		flexuosa.	*niyra.*	*inermis.*	*ornata.*	*spiritus.*	*helleri.*	*arenosa.*	*Parkeri.*	*mediterranea.*	*lingvura.*	*gibbosa.*	*angusta.*		
Neural Group.															
Supra-cerebral . .	Brain	× ×	—	—	—	—	—	—	—	—	—	—	—	—	—
I. Antenna . . .	Ant^1	× ×	—	—	—	× ×	—	—	—	—	—	—	—	—	× ×
II. Antenna . . .	Ant^2	× ×	× ×	× ×	× ×	—	× ×	× ×	× ×	—	—	—	—	—	× ×
Mandibular . . .	Mand	—	—	—	—	—	—	—	—	—	—	× ×	× ×	—	—
1st maxilla . . .	Mx_1	×	×	×	×	× ×	—	× ×	× ×	×	×	—	—	× ×	× ×
2nd ,, . .	Mx_2	×	—	—	—	×	×	×	×	—	—	—	—	—	×
1st thoracic . . .	T_1	× ×	—	—	× ×	—	—	—	—	—	—	× ×	× ×	—	—
2nd ,, . . .	T_2	× ×	—	—	—	—	—	—	—	—	—	—	—	× ×	—
3rd ,, . . .	T_3	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	—	—	—	× ×
4th ,, . . .	T_4	× ×	—	—	—	—	—	—	—	—	—	× ×	× ×	—	—
5th ,, . . .	T_5	× ×	—	—	—	—	—	—	—	—	—	—	—	—	—
6th ,, . . .	T_6	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	—	—	× ×	× ×
7th ,, . . .	T_7	× ×	—	—	—	—	—	—	—	—	—	× ×	× ×	—	—
8th ,, . . .	T_8	× ×	× ×	—	—	—	× ×	× ×	× ×	×	×	—	—	—	× ×
1st abdominal . .	Ab_1	× × ×	× ×	×	×	×	×	×	×	×	×	×	×	×	×
2nd ,, . .	Ab_2	× × ×	× ×	×	×	×	×	×	×	×	×	×	×	×	×
3rd ,, . .	Ab_3	× × ×	× ×	×	×	×	×	×	×	×	×	×	×	×	×
4th ,, . .	Ab_4	× × ×	× ×	×	×	×	×	×	×	×	×	×	×	×	×
5th ,, . .	Ab_5	× × ×	× ×	×	×	×	×	×	×	×	×	×	×	×	×
6th ,, . .	Ab_6	×	×	×	×	×	×	×	×	×	×	—	—	×	×
Anal	Ab_6	×	×	×	×	×	×	×	×	?	?	?	?	—	× ×
Visceral Group.															
1st gastric . . .	—	×	×	×	×	×	×	×	×	?	×	?	?	—	—
2nd ,, . . .	—	×	×	×	×	×	×	?	?	×	×	?	?	—	—
Pre-cardiac . . .	T_3	×	×	×	×	×	×	×	×	×	×	×	×	—	×
Post-cardiac . .	T_6	×	×	×	×	×	×	×	×	?	?	?	?	—	×
Intestinal . . .	Ab_1–Ab_6	2 in each segment	ditto	1 in each segment	?	?	?	?	?	?	?	?	?	—	—
Caudal Group.															
8th thoracic . .	T_8	×	×	×	×	×	×	×	×	—	—	×	×	—	—
1st abdominal . .	Ab_1	×	×	×	×	×	×	×	×	—	—	—	—	—	× ×
2nd ,, . .	Ab_2	×	×	×	×	×	×	×	×	—	—	—	—	—	× ×
3rd ,, . .	Ab_3	×	×	×	×	×	×	×	×	—	—	—	—	—	× ×
4th ,, . .	Ab_4	×	×	×	×	×	×	×	×	—	—	—	—	—	× ×
5th ,, . .	Ab_5	×	×	×	×	×	×	×	×	—	—	—	—	—	× ×
6th ,, . .	Ab_6	×	×	×	×	×	×	×	×	—	—	—	—	—	× ×
Accessory Group.															
Optic	Eye stalk	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×

× = median. × × = a pair. = undetermined. — = unrepresented.

TABLE II.—ARRANGEMENT OF CHROMOTOPHORES IN DECAPOD LARVÆ AND ADULTS.

Primary system.	Segment.	*Crangon vulgaris.*			*Hippolyte varians.*			*Palæmon squilla.*		*Carcinus mænas.*		*Macromysis flexuosa.*
		Zoea.	Mysis-stage.	Adult.	Zoea.	Adolescent.	Adult.	Zoea.	Adult.	Zoea.	Megalopa.	
Neural Group.												
Supra-cerebral or ad-rostral	Brain	—	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×
1st antennary . .	Ant[1]	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×
2nd ,, . .	Ant[2]	× ×	× ×	× ×	× ×	× ×	× ×	× ×	× ×	—	× ×	× ×
Sub-cerebral . . .	Brain	—	—	—	×	×	×	—	×	—	—	—
Labrum	—	× ×	× ×	× ×	×	×	×	—	?	×	×	—
Mandibular . . .	Mand	—	—	?	—	—	—	—	?	×	×	—
1st maxilla . . .	Mx_1	× ×	× ×	× ×	×	×	×	× ×	× ×	×	× ×	×
2nd ,, . . .	Mx_2	× ×	× ×	× ×	—	—	× ×	× ×	× ×	—	×	×
1st thoracic . . .	T_1	—	—	—	× ×	× ×	× ×	—	?	—	—	× ×
2nd ,, . . .	T_2	—	—	—	—	× ×	× ×	—	?	—	—	× ×
3rd ,, . . .	T_3	×	×	×	—	—	—	—	?	—	× ×	× ×
4th ,, . . .	T_4	—	—	?	—	—	—	—	?	—	—	× ×
5th ,, . . .	T_5	—	—	?	—	× ×	× ×	—	?	—	—	× ×
6th ,, . . .	T_6	—	×	?	—	× ×	× ×	—	?	—	—	× ×
7th ,, . . .	T_7	—	—	?	—	× ×	× ×	—	?	—	—	× ×
8th ,, . . .	T_8	—	—	?	—	× ×	× ×	—	?	—	—	× ×
1st abdominal . .	Ab_1	×	×	×	—	× × × × × ×	a group	—	×	× ×	× ×	× × ×
2nd ,, . .	Ab_2	×	×	×	—	,,	,,	—	×	× ×	× × × ×	× × ×
3rd ,, . .	Ab_3	×	×	×	—	,,	,,	—	×	× ×	× × × ×	× × ×
4th ,, . .	Ab_4	×	×	×	—	,,	,,	—	×	× ×	× × × ×	× × ×
5th ,, . .	Ab_5	×	×	×	—	,,	,,	—	×	× ×	× × × ×	× × ×
6th ,, . .	Ab_6	×	×	×	—	,,	,,	—	×	× ×	× ×	× × ×
Anal.	Ab_6	×	×	×	× ×	× ×	× ×	× ×	× ×	×	×	×
Visceral Group.												
1st gastric	—	—	?	?	—	×	×	—	× ×	×	×	×
Hepatic	—	—	?	?	× ×	× × × ×	× × × ×	× × × × × × represented by several secondary centres	several	—	—	×
Pre-cardiac . . .	T_3	—	× ×	—	—	×	×		,,	×	×	×
Post-cardiac . . .	T_6	—	×	—	—	×	×	,,	,,	×	×	×
Intestinal	Ab_1–Ab_5	—	?	?	—	×	×	,,	,,	—	?	2 in each segment
Caudal Group.												
8th thoracic . . .	T_8	—	×	×	—	×	×	—	?	—	—	×
1st abdominal . .	Ab_1	×	×	×	×	×	×	—	?	—	—	×
2nd ,, . .	Ab_2	×	×	×	×	×	×	—	?	—	—	×
3rd ,, . .	Ab_3	×	×	×	× × ×	× × ×	× × ×	× × ×	× × ×	—	—	—
4th ,, . .	Ab_4	× × ×	× × ×	× × ×	—	× × ×	× × ×	—	?	—	—	×
5th ,, . .	Ab_5	× ×	× ×	× ×	× ×	× ×	× ×	×	?	—	—	×
6th ,, . .	Ab_6	—	×	×	—	—	—	—	?	—	—	×
Optic	Eye stalk	—	× ×	× ×	—	× ×	× ×	× ×	× ×	× ×	× ×	× ×

TABLE III.—Tissue-reactions of *Hippolyte varians*. St. Vaast, Normandy. August 9 and 10, 1899.

	Muscle.			Percentages.				Liver.		
				Muscle.		Liver.				
	Alk.	Acid.	Alk. and acid.	Alk.	Acid.	Alk.	Acid.	Alk.	Acid.	Alk. and acid.
August 9.										
Morning . . . 10.30–12.	9	0	0	100	0	66	33	6	3	0
Afternoon . . . 2.30–3.30.	7	0	0	100	0	0	100	0	7	0
Evening . . . 8.50 P.M.	2	0	0	100	0	0	100	0	2	0
August 10.										
Morning . . .	—	—	—	—	—	—	—	—	—	—
Afternoon . . . 5.45–6.45.	11	0	0	100	0	54	36	6	4	(1 neutral)
Evening . . . 8.30.	3	4	(1 neutral)	33	44	11	89	1	8	—

TABLE IV.—Tissue-reactions of *Hippolyte varians*. Piel, June, 1900.

	Muscle.			Liver.		
	Alk.	Acid.	Acid and alk.	Alk.	Acid.	Acid and alk.
Morning . . 9–12.	17	0	2	14	1	4
Afternoon . . 12–7.30.	11	1	8	10	1	8
Evening . . 7.30–11.30.	11	2	12	8	10	5
	Proportion of alk. records to acid and acid and alk. records.			Proportion of alk. records to acid and acid and alk. records.		
Morning . .	17 : 2 = 90 per cent. : 10 per cent.			14 : 5 = 74 per cent. : 26 per cent.		
Afternoon . .	11 : 9 = 55 „ : 45 „			10 : 9 = 53 „ : 47 „		
Evening . .	11 : 14 = 44 „ : 56 „			8 : 15 = 35 „ : 65 „		

TABLE V.—*Hippolyte varians.* Piel (Lancashire), July 2–6, 1900.

	Muscle.				Liver.			
	Alk.	Acid.	Both.	Alk.	Alk.	Alk.	Acid.	Both.
				per cent.	per cent.			
Morning	3	0	0	100	100	3	0	0
Afternoon	5	0	0	100	80	4	1	0
Evening	7	0	1	87	62	5	—	3

TABLE VI.—Tissue-reactions of *Hippolyte varians.* St. Vaast, Normandy, 1899.

A.—Diurnes and Nocturnes.

	Diurnes.			Nocturnes.		
	Alk.	Acid.	Alk. and acid.	Alk.	Acid.	Alk. and acid.
August 1. Muscle	14	0	0	0	6*	—
August 4. Muscle	2	0	2	3	7	0
August 1. Liver	Not tested.			Not tested.		
August 4. Liver	1†	—	—	—	3‡	—
Totals :— Muscle	16 alk. : 2 acid and alk.			3 alk. : 13 (or 14) acid.		
Liver	1 alk. (1 only examined).			3 acid (3 examined).		

* 7 examined, 1 neutral or faint acid. † 1 only examined. ‡ 3 examined.

B.—Partially or wholly recovered Nocturnes.

	Alk.	Acid.	Alk. and acid.
Muscle	0	5	0
Liver	0	4	0

TABLE VII.—Tissue-reactions of *Mysis nigra*. Piel, July 2–5, 1900.

A.—In Normal (Black) Colour-phase.

Time.	Sex.	Colour.	Muscle.	Liver.	Blood.
July 4, 11 A.M. Fresh caught .	♀	Black	Alk.	Alk.	Alk. (blue).
" " " .	♀	"	"	"	" "
" " " .	♀	"	"	"	" "
" " " .	♀	"	"	Alk. and trace acid (? from ovary	" (colourless).
July 2, 6 P.M. " .	♂	Black to transp. dorsally	"	Acid	" (faint blue).
" 11 P.M. " .	♀	Black	"	Very alk.	" (blue).
July 4, afternoon	♂	Dark brown (trace blue dorsally)	"	Alk.	" (colourless).
" "	♂	" "	"	"	" "
Summary		—	All alk.	$\frac{7}{8}$ alk.	All alk.

B.—In Transparent Green or Blue Colour-phase.

Time.	Sex.	Colour.	Muscle.	Liver.	Blood.
July 4. In porcelain vessel with muslin cover from 11–1.30 P.M. Examined 1.30	♀	Green	Alk.	Acid	Alk. (blue).
" " "	♀	"	"	Acid (trace)	" "
" " "	♀	"	"	Acid	" "
July 2, 6 P.M.	♀	Transp. blue	"	"	" "
July 3. In porcelain since 4 P.M. July 2. Examined 12 NOON	♀	Pale blue	Alk. (blue in colour)	"	" "
Summary		—	All alk.	*All acid*	All alk.

TABLE VIII.—Tissue-reactions of *Mysis flexuosa*. Piel, July 2–5, 1900.

A.—In Normal Brownish Phase.

Time.	Sex.	Colour.	Muscle.	Liver.	Blood.
July 3, 8 P.M.	♀	Transp., slight brown tinge	Alk.	Alk.	Alk., colourless.
July 5, 5.15 P.M.	♀	Brownish	,,	,,	,, ,,
,, ,,	♂	,,	,,	Acid	,, ,,
July 6, 9.30 A.M.	♀	,,	,,	Trace acid	,, ,,
,, ,,	♀	Light brown	,,	Acid	,, ,,
Summary		—	All alk.	2 alk. : 3 acid	All alk.

B.—In Transparent Phase.

Time.	Sex.	Colour.	Muscle.	Liver.	Blood.
July 2, 12 NOON	♂	Transp., greenish	Alk (faint)	Acid	Alk. and colourless.
July 3, 8 P.M.	♀	Transp.	Alk.	Alk.	,, ,,
July 5, 2.30 P.M. Porcelain effect	♀	Transp., colourless	,,	Acid	,, ,,
,, ,, ,,	♀	,, ,,	,,	,,	,, ,,
,, ,, ,,	♀	,, ,,	,,	,,	,, ,,
,, 5 P.M. In dark from 2.50	♀	,, ,,	,,	,,	,, ,,
,, ,,	♀	,, ,,	,,	,,	,, ,,
,, ,,	♀	,, ,,	,,	,,	,, ,,
Summary		—	All alk.	1 alk. : 7 acid	All alk.

TABLE IX.—Movements of Various Crustacea in Relation to Light.

	In transparent jar.	On *white* background.	On *black* background.	Choice of background.
Palæmon, adult	? –	–	–	Black
,, zoea	+	+	? +	White
Hippolyte, adult	? =	+	+	,,
Hippolyte fuscigera, zoea	+	+	?	,,
Mysis flexuosa adult	+	–	+	Black
Mysis inermis	+	–	+	? ,,

– = Movement away from the illuminated region.
+ = ,, toward the illuminated region.
= = ,, indifferent.
? = ,, uncertain.

For description of method of experimentation see Text p. 345–346.

TABLE X.—Periodicity Table. Zoeæ of *Palæmon.*

Hatched August 23, 1901. Tregastel.
72 zoeæ, August 24, put and maintained in the dark.

	24th.				25th.		
	9.35 A.M.	10.37 A.M.	1.40 P.M.	10.30 P.M.	9.45 A.M.	2.20 P.M.	10.30 P.M.
Condition of T pigments.	0	0	0 (with very slight +)	0	+ (some 0)	+ fair	0 (in few slight +

	26th.			27th.		28th.
	9.30 A.M.	1.50 P.M.	3.50 P.M.	9.30 A.M.	5.30 P.M.	9.15 A.M.
Condition of T pigments.	0 in most (slight in few)	0	0	0 ×	0	0

T pigments = those of red series viewed by transmitted light.
0 = pigments contracted.
+ = pigments expanded.
× = zoeæ have reached stalk-eye stage ; at this time much diffuse blue substance makes its appearance about the chromatophore-centres and persists ; animals active.

TABLE XI.—Table Recording Movements of Chromatophore-pigments of *Hippolyte*-zoeæ in White and in Monochromatic Light on Scattering (White) and Absorbing (Black) Backgrounds. Roscoff, August 1, 1901.

Starting point = mid phase (induced by clear glass).	Nature of the light employed.		Background.			
			White.	Black.	Black.	White.
			10–2.30 P.M. = $4\frac{1}{2}$ hrs.	2.30–6.15 P.M. = $3\frac{3}{4}$ hrs.	6.15–8.30 A.M. = $14\frac{1}{4}$ hrs.	8.30–2 P.M. = $5\frac{1}{2}$ hrs.
T slight +	White	T	0 (some) + slight (some)	+ ?	0	+
R slight +		R	+	+ five	+ five thorax 0 abdomen	+
T slight +	Red	T	+ slight on head 0 on tail	0	0	0
R slight +		R	0	+ fair and branchial and mandibular other chromatophores 0	+ fair stomachic 0 the rest	0 (+ fair in 1)
T slight +	Orange	T	0	0	0	+ fair
R slight +		R	0 (except slight + on mandibular)	+ fair on head 0 on tail	0	0 + slight on stomachic
T slight +	Green	T	0	?	0	0
R slight +		R	+ slight on head 0 on tail	0 + slight branchial and mandibular	0 + slight stomachic	0
T slight +	Blue	T	0	0	+ slight	dead
R slight +		R	+	+ fair on head and anal 0 the rest	+ very slight 0 in 1	

0 = contraction
+ = expansion.

T = the record made by transmitted light } 12 animals used in each experiment.
R = „ „ reflected „

TABLE XII.—Reactions of Pigments of *Hippolyte varians* (Adult) to White and Monochromatic Light combined with Scattering (White) and Absorbing (Black) Backgrounds. Roscoff, July 9, 1901.

To be compared with Table XI. of Larval Reactions. T records only.

Nature of light employed.	Background.			
	White background.	Black. 4.15 P.M.	Black. 8.15 P.M.	Black. 8.15 A.M.
White, open . .	T 0	+	+	+
White (pinhole) .	T 0	{ + (2) 0 (1)	} +	+
Red	T 0	+	+	]
Orange	T 0	+ fair	0	+
Green	T 0	{ + head and tail 0 mid.	} +	+
Blue	T 0	(–)	(–)	(–)

+ = expansion. T = examined by transmitted light.
0 = contraction. (–) = not recorded.

TABLE XIII.—Recording Pigment-movements of *Palæmon* zoeæ in Monochromatic Light on (White) Scattering Background. Tregastel, August, 1901.

Reaction of adults.	Nature of the light employed.	Reaction of zoeæ.					
		Started from dark phase. 26th.			27th.		28th.
		2.25 P.M.	3.50 P.M.	7.30 P.M.	9.30 A.M.	5.30 P.M.	9.15 A.M.
T 0	Red T	0	+	+ (slight)	+ good	+ fair	(0 sick)
R 0	Red R	0	+	+ slight	+ 0 dorsal + ventral	0 dorsal + ventral	0
T 0	Orange T	0	+	+ fair and slight	+	+ fair	+ slight
R 0	Orange R	0	+	+ fair	+ fair In others 0 dorsal + ventral	+ good	0 dorsal + ventral
T 0	Green T	0	+	+ fair	+	0	0 (sick)
R 0	Green R	0	+	+ fair	+	0	0
T 0	Blue T	0	+	+ fair	+	+ slight	0 (sick)
R 0	Blue R	0	+	+ fair	+	+ good	0
T 0	White T	0	+	+	} sick	—	—
R 0	White R	0	+	+			
T +	White Black ground T	0	+	+ fair	+	+	+ } active
T +	White Black ground R	0	+	+ fair	+	+ ventral 0 dorsal	+

0 = contraction. T = T pigments recorded by transmitted light.
+ = expansion. R = R ,, ,, reflected ,,

TABLE XIV.—Table of Reactions of *Palæmon*-zoeæ to Feeble White Light (admitted through pinholes in cover of vessel) combined with Porcelain (White) and Black Background. Tregastel, August 24th, 1901. Zoeæ watched on 23rd.

Time.	Porcelain (white).		Black background.	
	(T) pigments.	(R) pigments.	(T) pigments.	(R) pigments.
24th, 9.35 A.M. . . (initial phase)	+	+	+	+
24th, 10.37 A.M .	+ fair (5) 0 (3)	(–)	+ (8) 0 (3)	(–)
„ 1.40 P.M. . .	+		+	
„ 8 P.M. . . .	0 (+slight maxillary in some)	(–)	0 in half + slight maxillary in half	(–)
25th, 9.45 A.M. . .	+	(–)	+	+
„ 2.20 P.M. . .	+	+	+	+
Lamp lit at 7.30 P.M.	+ in half			
25th, 9 P.M. . . .	+ slight half	(–)	+ (good)	(–)
„ 10.30 P.M. .	(–)	(–)	+ fair	(–)
26th, 9.30 A.M. . .	+	+	+	+
„ 7.30 P.M. . . .	+ fair	+ fair	(–)	(–)
27th, 9.30 A.M. . .	+ ⎫ + ⎬ = numbers 0 ⎭		+	0 dorsal + fair ventral
28th, 9.15 A.M. . .	eye-stalks not devd. 0 [sick]	0	eye-stalks developed – [well]	(–)
29th, 3 P.M. . . .	eye-stalks developed 0 dead	0	+	+
30th, 9.45 A.M. .			⎧ + ⎨ + ⎩ 0	+ most active 0 less active 0 dying and dead

Cf. with adult *Palæmon* which gives constant "reaction to background," contraction on white, expansion on black background (Table XV.).

Controls started at the same time, show *Palæmon* zoeæ in porcelain open vessels, T + R +; and in black ground open vessels T + R +.

+ = expansion.

0 = contraction.

(–) = not recorded.

T pigments = red transmitting.

R pigments = yellow, &c., reflecting substances.

TABLE XV.—*Palæmon squilla.* Reactions of Chromatophore-pigments to White and to Monochromatic Light, combined with Scattering (White) and Absorbing (Black) Background. Tregastel, April 7 and 8, 1902.

White background.		Black background.			White background.
7th, 11.30 A.M.	2.30 P.M.	3.45 P.M.	4.40 P.M.	8th, 9.45 A.M.	10.45 A.M.
(1) White light .	Transparent :— Red pigment, 0 Yellow ,, 0 Blue ,, 0	Some expansion :— Red, slight + Yellow, fair + Blue, 0	Expansion as at 3.45	Expansion :— Red, fair + Yellow, good + Blue, 0	Transparent, *i.e.* :— Red, 0. Yellow, 0. Blue, + (temporary blue phase).
(2) Red . . .	Transparent (more so than (1),(3),(4),(6)):— Red, 0 Yellow, 0 Blue, 0	Slight expansion :— Red, very slight + Yellow, slight + Blue, 0	Expansion as at 3.45	Expansion as at 3.45 (less expansion than (1), (3), (4), (5))	Transparent.
(3) Orange . .	Transparent :— Red, 0 Yellow, slight + Blue, 0	Expansion (more than (1). (2), (4), (5)) :— Red, + Yellow, + Blue, 0	Expansion as at 3.45	Expansion as at 3.45	Transparent.
(4) Green . .	Transparent (temporary blue phase) :— Red, 0 Yellow, 0 Blue, +	Some expansion :— Red, 0 Yellow, fair + Blue, fair +	Fair expansion :— Red, slight + Yellow, fair + Blue, very slight +	Expansion :— Red, fair + Yellow, good + Blue, 0	Transparent.
(5) Blue . .	Transparent :— Red, 0 Yellow, slight + Blue, 0	Fair expansion :— Red, slight + Yellow, fair + Blue, 0	Fair expansion as at 3.45	Expansion :— Red, + Yellow, good +	Transparent.

0 = contraction of pigment into chromatophore centres.
+ = expansion ,, ,, ,, branches.

TABLE XVI.—*Macromysis inermis* and *Palæmon squilla.* Mysis Experiments, Cullercoats, July 17, 1900; Palæmon Experiments, Tregastel, April, 1902. Reactions of the Chromatophore-pigments to Normal and Inverted Light-conditions.

Backgrounds used:—Black (absorbing), mirror (reflecting), and white (scattering). Lights used in conjunction with these several backgrounds:—White, red, green, and blue.

0 = contraction. + = expansion of pigment. T = the light-transmitting series of pigments.

Light.	Black (absorbing) background.		Mirror background.		White (scattering) background.	
	Normal. Illumination from above background below.	Inverted. Illumination from below "background" above.	Normal. Illumination from above background below.	Inverted. Illumination from below "background" above.	Normal. Illumination from above background below.	Inverted. Illumination from below "background" above.
White—						
Macromysis inermis	(T) +	(T) +	(T) fair +	(T) fair +	(T) 0	(T) 0
Palæmon squilla .	+	+	Fair +	Fair +	0	0
Red—						
Macromysis inermis	(T) +	(T) +	(T) fair +	(T) fair +	(T) 0	(T) 0
Palæmon squilla .	+	+	Fair +	Fair +	0	0
Green—						
Macromysis inermis	(T) +	(T) +	(T) fair +	(T) fairish +	(T) 0	(T) 0
Palæmon squilla .	+	Not recorded	Not recorded		Not recorded	
Blue—						
Macromysis inermis	+	Not recorded	Not recorded		(T) 0	Not recorded
Palæmon squilla .	+	+	Fair +	Fair +	(T) 0	(T) 0

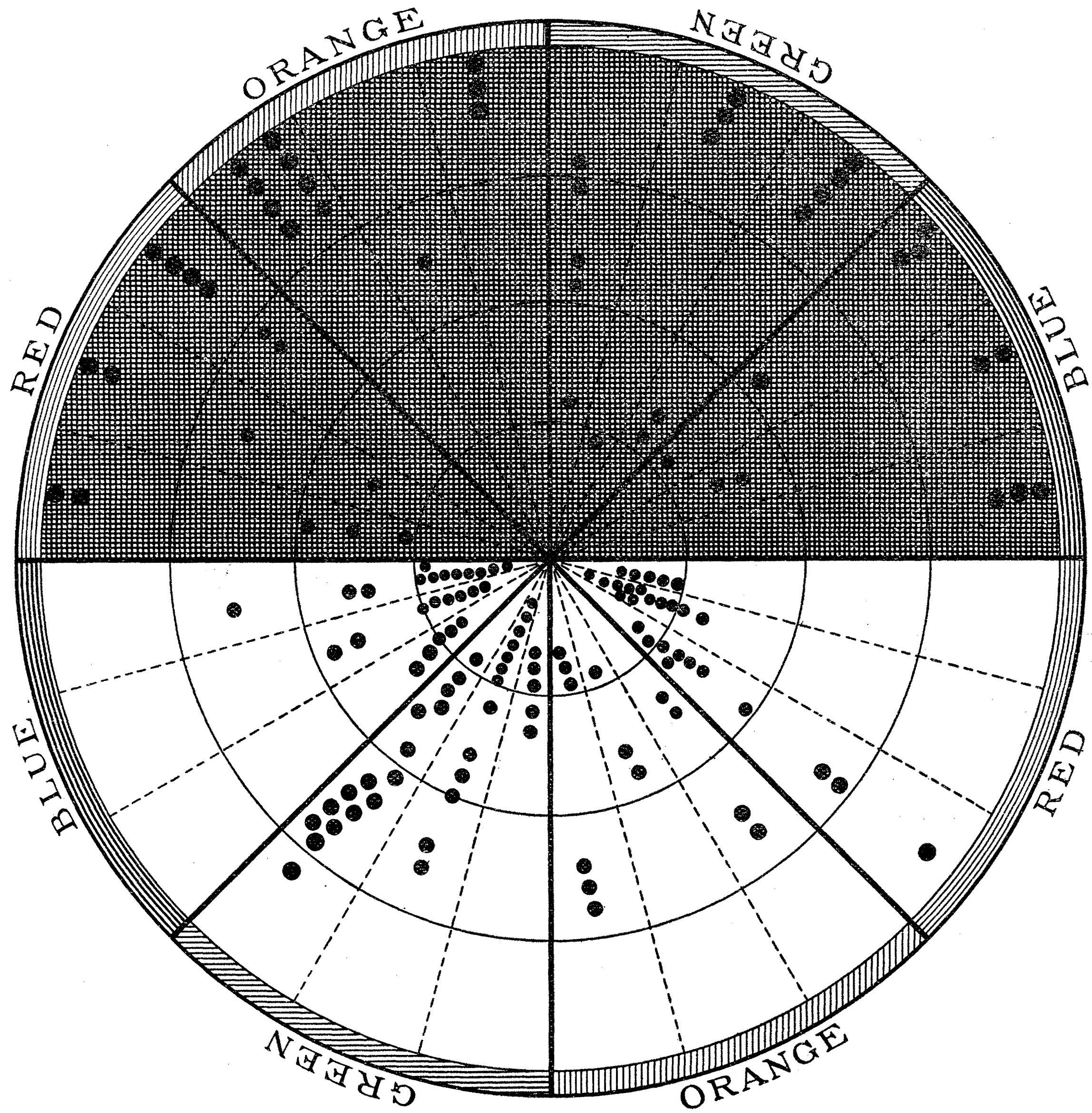
STATISTICAL Table (to face Target Diagram). *Macromysis inermis.*

Total Reactions to Monochromatic (Red, Orange, Green, and Blue) Light acting in conjunction with—

	A "white," scattering, ground.		A "black," absorbing, ground.	
	Totals.	Percentages in round numbers.	Percentages in round numbers.	Totals.
Full contraction (inners)	50	51	2	1
Fair contraction = Slight expansion (inner-mids) .	26	27	19	10
Slight contraction = Fair expansion (outer-mids) . .	19	19	15	8
Full expansion (outers)	2	2	63	24
Combining inners with inner-mids and outers with inter-mids we get—				
Full or fair contraction	76	78	21	11
Fair or full expansion.	21	21	78	32

TARGET DIAGRAM.

Each dot represents an animal; the dots in the "bull" represent animals whose chromatophores have contracted as a result of light-stimulation; those in the outer ring, animals whose chromatophores expanded on stimulation; intermediate dots



show intermediate results. The names round the rim of the target—red, orange, green and blue—indicate the monochromatic lights used in the experiments; all results obtained with red light, for example, are recorded in the two opposite sections; and so on for the other colours.

Each sector is subdivided into three; starting from the top (red sector) of the

right-hand side, the first subdivision (nearest the equator) contains records of experiments with animals previously in the dark (contracted) phase; the second subdivision, those of experiments with animals previously in the porcelain (contracted) phase; the third subdivision, those with animals previously in the dark background (expanded) phase. And so on, clockwise.

A mode of representing the pigment-movements of *Macromysis inermis* in response to monochromatic lights. On the white half, are the results produced by the monochromatic lights acting in conjunction with a scattering (white) background; on the shaded half, those produced by the same lights acting in conjunction with an absorbing (black) background.

The screens used for monochromatic light and rays transmitted by the various light-filters employed are given below :—

Red.—(1) Landolt-screen (1894) of two troughs, each 20 millims. wide, the first filled with "crystall-violett 5 BO" (·05 *g* in dilute alcohol), the second with potassium chromate 10 per cent This screen transmits from 718–639$\mu\mu$.

(2) Red glass. Selected pieces from Mr. CHAPMAN of Manchester. Transmit nearly pure red. Two sheets of BAKER's red gelatine give a pure red.

Orange.—Nagel-screen (1898), copper acetate and safranin = 640–600$\mu\mu$.

Yellow.—Landolt-screen. Three troughs: 30 per cent. nickel sulphate in first, 20 millims. thick; 10 per cent. pot. chromate in the second, 15 millims. thick; and ·025 per cent. pot. permanganate in the third, 15 millims. thick. This gives 614–574$\mu\mu$, but is a very troublesome screen to keep in order.

Green.—(1) Landolt-screen. Two troughs, each 20 millims. thick. In the first 60 per cent. copper chloride, containing two molecules of water of crystallisation. In the second a 20-per-cent. solution of pot. chromate. A very pure green.

(2) Three layers of BAKER's green gelatine plates transmit pure green.

Blue.—(1) Landolt-filter two troughs, each 20 millims. width. The first filled with "crystall-violett 5 BO," ·005 per cent. The second with copper sulphate 15 per cent. Transmits 478–410$\mu\mu$. Dark blue.

(2) Nagel-filter of ammoniated copper sulphate, transmits from F to end of violet.

After these experiments were made, we found references to more recent methods for obtaining monochromatic light in "Encyclopædie der mikroskopischen Technik," 'Art. Mikrophotographie' (1903, pp. 853–855), which are worth a careful trial by those who are undertaking investigations of this kind.

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EXPLANATION OF PLATES.

COMMON REFERENCE LETTERS.

Ant and ant_2 : 1st and 2nd antennæ. Ab : Abdominal segment.
Br : Supra-cerebral chromatophores.
Car : Carapace-centres (secondary).
Caud : Caudal-group of primary chromatophores.
Fibr : Fibrous matter of nerve cord.
G : Stomach.
Gang : Ganglion cells.
G_1 : Gastric chromatophore.
H : Heart.
Hep : Paired hepatic centres.
La : Labrum.
Mn : Mandible.
Mx_1, Mx_2 : 1st and 2nd maxillæ and their chromatophores.
Neur : Neural group of centres.
Oc : Chromatophore on optic stalk.

Pre-card : Pre-cardiac visceral chromatophore-centre.
Post-card : Post-visceral chromatophore-centre.
T_1, etc. : Thoracic segments.
Visc : Visceral chromatophores.

The diagrammatic figures are so coloured that the primary chromatophore system is black, the secondary one red.

PLATE 18 (× 15).

Fig. 1. *Macromysis nigra* n. sp. Dorsal surface seen with the pigment contracted.

Fig. 2. The same seen with the pigment and reflecting substance fully expanded. The figure shows the typical form of branching of Mysidean chromatophores, especially the long branches from the neural centres (Mx_1, T_3), and the branches on the optic stalk (Oc.).

Fig. 3. The same to show the reflecting substance on a dark background. In this species it does not assume a definite pattern. Contrast with *M. flexuosa*, Plate 21, fig. 18C, where the definite pattern is expressed.

PLATE 19 (× 15).

Fig. 4. *Macromysis nigra* n. sp. seen from the ventral surface with the pigment contracted.

Fig. 5. The same with the pigment expanded.

Fig. 6. Side view to show the elaborate branch-system of the neural chromatophores that supply the carapace and skin, and the branches of the caudal centres (A, B_1, etc.).

PLATE 20 (× 18).

Fig. 7. *Macromysis inermis.* Seen from the ventral surface with the pigment expanded (compare with Plate 21, fig. 16). The relation of the branches to the nerve-cord and its nerves is very clear.

Fig. 8. The same from the dorsal surface. The figure shows the visceral branch system on the stomach, and especially on the liver and gonad (Hep); also the branches from the neural centres near the rostrum, and at the sides of the carapace. The form of the abdominal caudal chromatophores is very constant, and each one contains greenish-yellowish reflecting substance arranged in branches as shown. The arrangement of blue spots over the liver is quite constant and due to branches from the hepatic median centre, Hep.

Fig. 9. *Macromysis inermis.* Dorsal surface to show the definite and characteristic colour-pattern of reflecting substance on a dark ground. The branch-system of the second gastric centre, the large pre-cardiac (Pre-card) or hepatic centre, and each abdominal centre, is provided with a supply of reflecting substances: white, blue, greenish-blue, and yellow. The total effect in life is one of great brilliancy.

PLATE 21.

Figs. 10–14 are embryos of three species of *Macromysis*: the figures show that the characteristic arrangement of the chromatophore-centres is attained before birth. The specimen here called *Macromysis nigra* is when mature, but not full-grown, identical with *M. neglecta.* Subsequently when full-grown it assumes appendicular characters identical with those usually given as diagnostic of *M. flexuosa.* Hence we have had to adopt neither of the names *neglecta* or *flexuosa*, and have given this *Mysis* a new name (*Nigra*). Its characteristic features are the possession of neural centres on T_3, T_6 and T_8, and double abdominal centres (see pp. 331, 332).

Figs. 10, 11. *Macromysis nigra* n. sp. Figs. 12, 13. *M. flexuosa.* Fig. 14. *M. inermis.*

Fig. 15. Side-view of the anterior portion of the body of *Macromysis flexuosa.* The figure is drawn from a moderately expanded specimen, and shows both the centre-system and the branch-system. The neural centres extend from BR to AB_2 Gang., and together with the appendages indicate the number of segments. G_1, G_2, Pre-card, Post-card and Int, are the visceral centres; T_8, Ab_1, &c., are the caudal ones. The relation of the branches of the large pre-cardiac centre to the gonad and liver-lobes is well-shown. This feature is common to the majority of Mysidæ. To a less degree, the post-cardiac visceral centre supplies the same organs, and the hinder border of the carapace in addition. Compare the text pp. 302, 303. × 10.

Figs. 16–18. Dorsal and ventral views of three species of *Mysis* (or *Macromysis*) to show their constant adult chromatophore-characters. By the aid of these figures it is easy to identify specimens. × 4.

Fig. 16C shows (in red) the extraordinarily close relation of the chromatophores to the nervous system. Fig. 20 is to be compared with fig. 16B to show the change which expansion and contraction of the pigments makes in the appearance of the animal.

Fig. 18C shows the distinctive colour-pattern of *M. flexuosa* which is due to the reflecting substance constantly expanding into the same channels and causing the same arborisations to appear.

Figs. 19–22 illustrate the structure, development and arrangement of the chromatophores of *Macromysis flexuosa* and *M. inermis.*

Fig. 19. A diagrammatic transverse section across the embryo of *Macromysis flexuosa* to show the relation of two of the three chief groups of chromatophores—neural and visceral—to the nervous system and other organs. The white dots in the chromatophores are the nulcei. The section is taken across the antennæ and maxillæ.

Fig. 20. Vertical sagittal section of three ganglia in *Macromysis flexuosa* (embryo 2 millims. long), to show the mode of origin of the abdominal neural chromatophores as sacs developed at the expense of the epidermis covering the ganglia. For the significance of this mode of origin, see the text, Section II., p. 305, and Section VII., p. 333.

Fig. 21. Vertical section (a little to one side of the median line) of an embryo of *Macromysis flexuosa*. The figure is intended to show the relation of the developing abdominal neural chromatophore-centres to the embryonic ganglion cells. The nuclei are indicated by white dots.

Plate 22.

Fig. 22. Two chromatophores and intervening glandular and vascular tissue from the brood lamellæ of *Macromysis inermis*. In one, pigment has been left at the centre. Compare the text, Section III., p. 308, and Section VII., p. 333.

Fig. 23. A chromatophore from the telson of *Macromysis flexuosa*. The figure shows the apparent independence of the constituent cells, the way they are inserted into the central sac (*Membr*), and their fibrillar structure. The glandular tissue (Gl) which is so constantly associated with the chromatophores and their branches is shown.

Fig. 23A. A "chromatophore" from the musculature of *Hippolyte varians* to show the peculiar endings.

Figs. 24–28 illustrate the development of the chromatophores in the crab.

Fig. 24. The zoea of the common shore-crab (*Carcinus mænas*) seen from the side, to show the primary and secondary chromatophore-systems. It may be usefully compared with fig. 35. × 50.

Figs. 25, 26. The zoea of the shore-crab *Carcinus mænas* before its first moult, seen from above (25) and from below (26). The neural centres are very strongly developed, and in the abdomen are not only paired, but send upwards a process which becomes virtually isolated (*N. dors*), and appears in the dorsal view. The secondary system is composed of two pairs of carapace-centres and of maxillipedal ones. These figures are to be compared with figs. 42 and 43, the zoea of *Hippolyte*, and still more instructively with *Mysis*, Plate 21, fig. 18. × 50.

Figs. 27, 28. The "*megalopa*-stage" of the shore-crab (*Carcinus mænas*) from the upper (27) and under (28) surfaces. The figures show that in spite of the

alteration in form and complexity as compared with the zoea, the crab has retained the zoeal chromatophore-system, and has merely subdivided the secondary chromatophores on the carapace : thus the primary system is not concealed as in *Hippolyte*, or *Crangon* by the secondary one, at least during the contracted phase. Later on, the individual centres of both systems merge into a sheet or double sheet of superficial inert masses. It will be noticed that the caudal group of primary chromatophores is absent (*cf.* text, Section IV., pp. 317–319). × 15.

Figs. 29–33 are drawings of the zoea-larva of *Palæmon squilla* showing dorsal and ventral views both of the expanded and contracted pigmentary phases. × 50.

Fig. 29 shows the two pairs of maxillary centres, with their elaborate branches of red pigment and green reflecting substance. The former branch up dorsally into the nervous tissues, and give rise to the splash of orange colour seen in the figure.

Fig. 30 shows the same animal from the upper surface. The splash of orange colour is seen through the optic ganglion. Along what will eventually be the frontal margin of the carapace, is an arborescent green marking due to the branches of both the supra-cerebal centres (Br) and of the deep antennary centres (Ant_2). The three pairs of centres on the carapace form the beginnings of the characteristic stripes of the adult. (See fig. 34.) There are three pairs of small hepatic centres and one pair of large ones (Hep).

Fig. 31. The dorsal surface of the same larva with the pigment contracted and the centre-system very distinctly shown. The anal chromatophores are the only neural centres present in the abdomen at this stage.

Fig. 32. The ventral surface showing the centres of the neural group of chromatophores ; to be compared with fig. 29.

Figs. 33, 34 show the origin of the characteristic colour-pattern of *Palæmon squilla* from its zoea-pattern. These figures also show how the neural primary group of chromatophores is developed in the late larval stage as in *Hippolyte*, and not in the early larva as in *Crangon*. The persistence of the large neural maxillary centres of the larva is also shown. The visceral system of chromatophores is omitted (fig. 34). × 12.

PLATE 23.

The figures on this plate illustrate the development of the primary and secondary systems of chromatophores in the Shrimp (figs. 35–40) and in *Hippolyte varians*. The former system is coloured black, the latter red. For the actual colouring see the text (Section IV.).

Fig. 35. The zoea of the Shrimp (*Crangon vulgaris*) seen from the side. The primary

centres are for the most part median, and some paired. Which are median and which are paired can be determined by reference to figs. 36, 37. × 43.

Figs. 36, 37. Zoea of the common Shrimp (*Crangon vulgaris*) to show the primary chromatophore-centres (black) and the secondary ones (red). These figures are to be compared with the views of *Mysis*, particularly *M. inermis*. Plate 21, fig. 16. Fig. 36 is the ventral view. Fig. 37, the dorsal one. × 40.

Fig. 38. Late-larval ("*Mysis*-stage") stage of the Shrimp. The figure shows that additions have been made both to the primary and secondary systems of chromatophores. The visceral centres (*Pre-card* and *Post-card*) have now appeared. × 15.

Fig. 39. Adolescent stage of *Crangon vulgaris* from a specimen 5 millims. in length. Dorsal view to show the manner in which the secondary system of chromatophores (red) arise on the carapace and pleura, and also the persistent primary caudal and visceral centres (black).

Fig. 40. Adult stage of *Crangon vulgaris* to show the relations of the primary and secondary systems of chromatophores. The former persists as well developed neural and caudal groups, but as a reduced visceral group.

Figs. 41–49 illustrate the development of the colour-pattern of *Hippolyte varians*.

Figs. 41–43. The zoea of *Hippolyte varians* to show the primary and secondary chromatophores, the former in black, the latter in red. The centre-system of this larva, like that of the larvæ of the other Decapods we describe, is perfectly constant. Each centre contains a red pigment and yellowish-green reflecting substance. When expanded into the branch system, filmy stellate patches are produced over the head, carapace and tail, and on the appendages and nerve-cord. By reflected light these patches appear greenish-white; by transmitted light they have merely a greyish tint. × 80.

Fig. 41 lateral view, fig. 42, ventral view, fig. 43, dorsal view.

Figs. 44–49 are intended to show how the three chief adolescent colour-patterns of *Hippolyte varians* are derived from the single and uniform pattern of the larva. (*Cf.* the text, Section V., pp. 324–328.) × 30.

Fig. 44 is an early adolescent phase (4–5 millims. long), and is a phase passed through by many, if not by all *Hippolyte varians* on their way to more distinctive patterns. The neural system is now complete, the visceral system is well-developed, and a secondary series of centres (red) have been developed in the carapace, at the bases of the gills and legs, and on the pleura of the tail. When expanded, this centre system gave the appearance of a faint brown-liner. Much of the reflecting substance of the larva is still present.

Fig. 45 shows how by hypertrophy of the intestinal visceral centres, and by the formation of secondary centres below the gut, across the tail-segments, around the liver and on the carapace, the "liner" colour-form is produced. It may be red, yellow, green or brown, with bars and spots of superficial reflecting substance.

Fig. 46 shows how by hypertrophy of secondary centres round the roots of the great vessels, the liver and gonad, a bar of colour is formed in the thorax; by increase in the number and size of the elements in the third segment of the tail, a second bar is formed. Thus the "barred" colour-form arises.

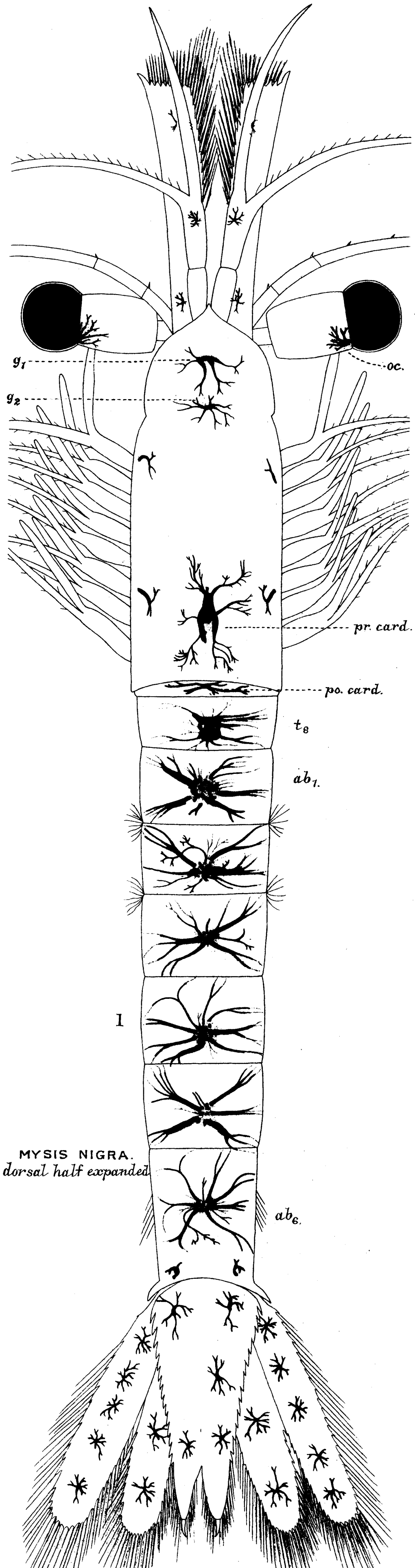
Fig. 47 shows how by the development of minute chromatophores scattered evenly in the muscle, on the viscera, nerve-cord and skin, one type of "monochrome" colour-form arises.

Fig. 48. Side view of the blotched colour-variety. The importance of this colour-form lies in the fact that it is based on an underlying "liner" pattern seen in fig. 45, and that it occurs in other species of Crustacea, for example in *Hippolyte cranchii* and *H. pusiola.* (See the text, Section V., p. 324.)

Fig. 49. Dorsal view of the "blotched" colour-form of *Hippolyte varians*, showing that the primary system may give rise indirectly to a part of the colour pattern, which in this case is formed in a very definite and segmental manner. Round the liver, on the carapace and pleura, bands of chromatophores arise.

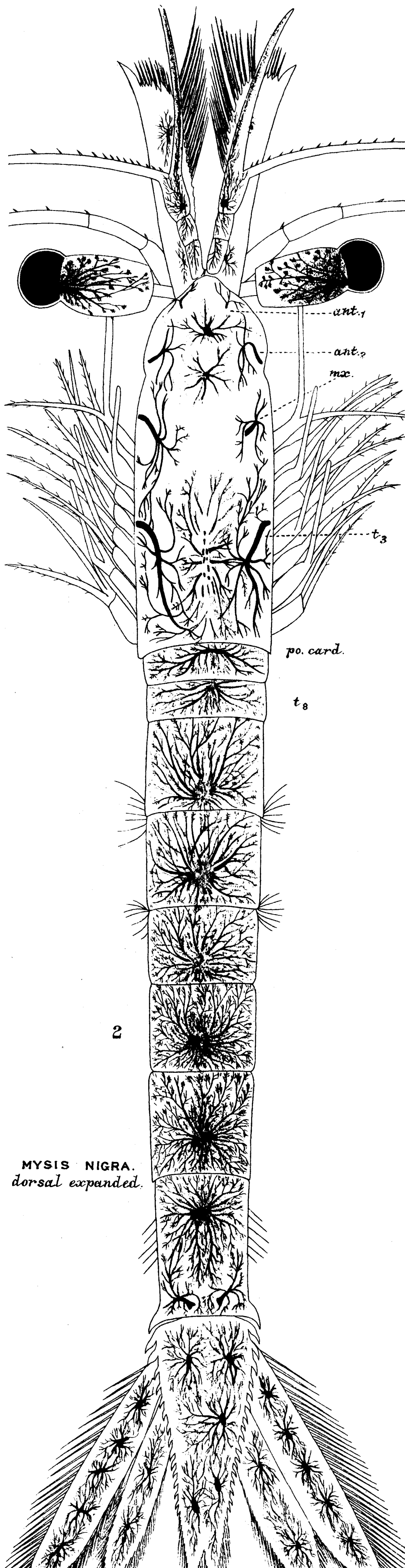
Figs. 50–52 are side views of *Hippolyte varians* (primary system of adolescent-stage), of *Mysis flexuosa* and of *Anaspides.* A comparison shows that the neural group of chromatophores occurs in all three animals at the base of the appendages; that a more restricted visceral group occurs in the *Hippolyte* and *Mysis* (*Pre-card*, *Post-card* and G_1, G_2); and that a caudal group occurs in all three genera.

The importance of *Anaspides* is referred to in the text (see p. 330), and it is introduced here to show diagrammatically how its chromatophore-system may be compared with that of *Mysis* and *Hippolyte.*



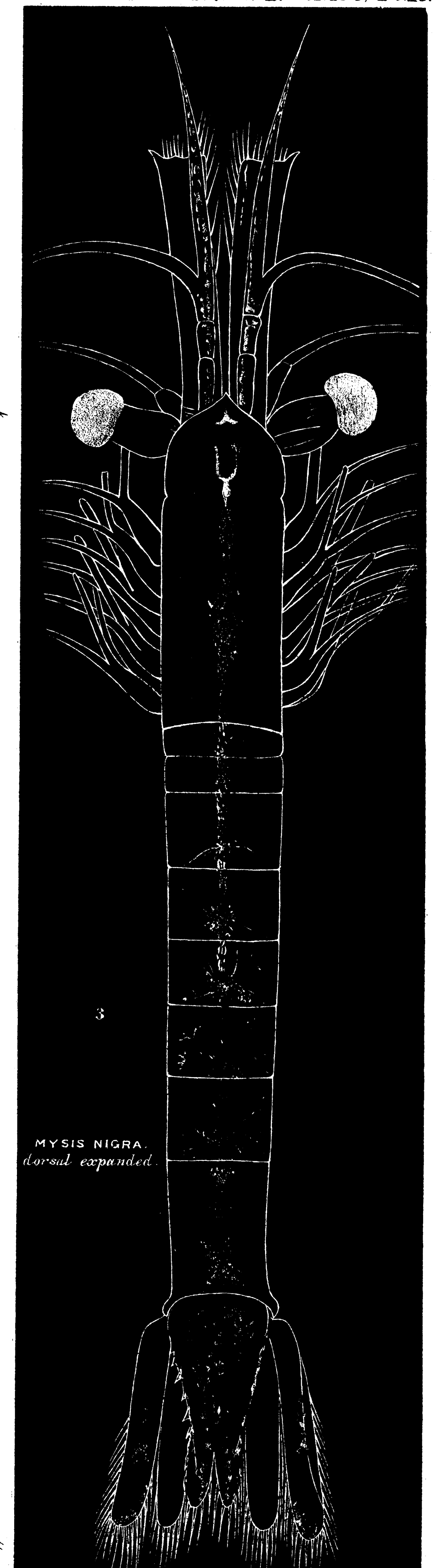
1

MYSIS NIGRA.
dorsal half expanded.



2

MYSIS NIGRA.
dorsal expanded.

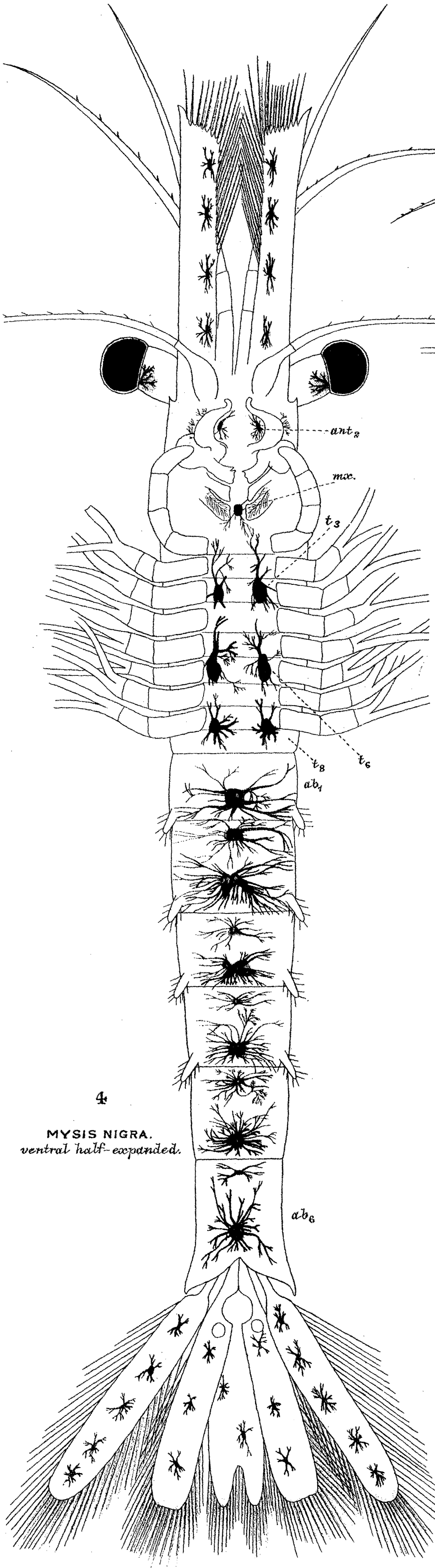


3

MYSIS NIGRA.
dorsal expanded.

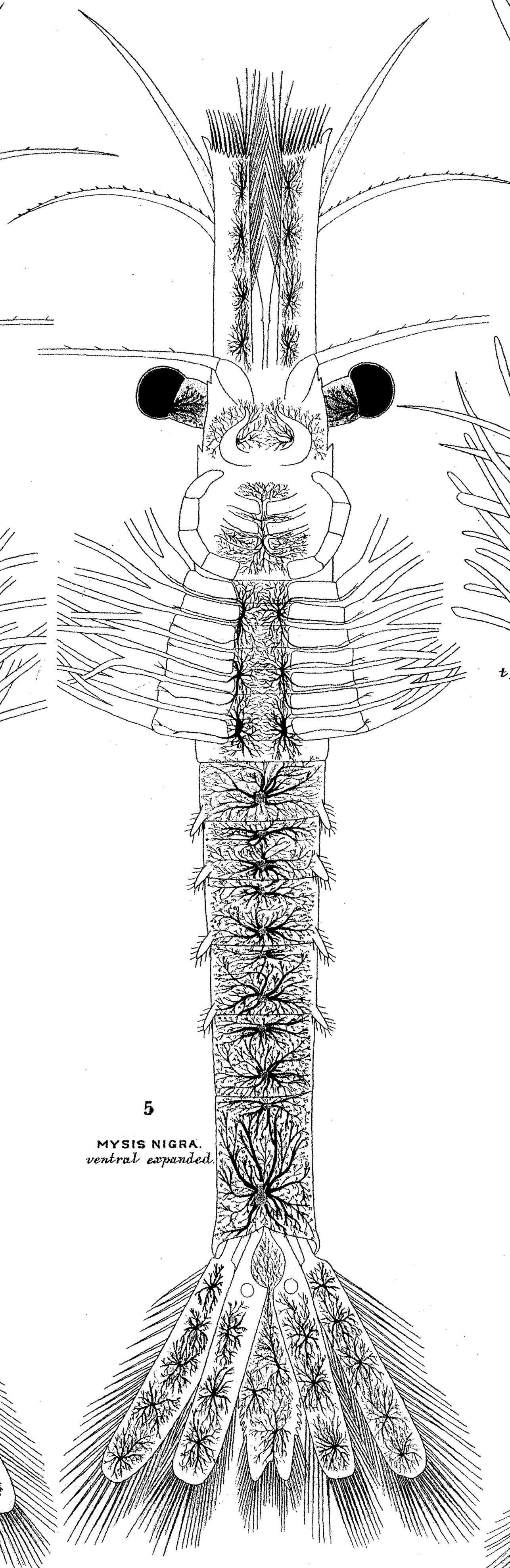
Miss D. Richardson del.
M. P. Parker lith.

Parker & West imp.



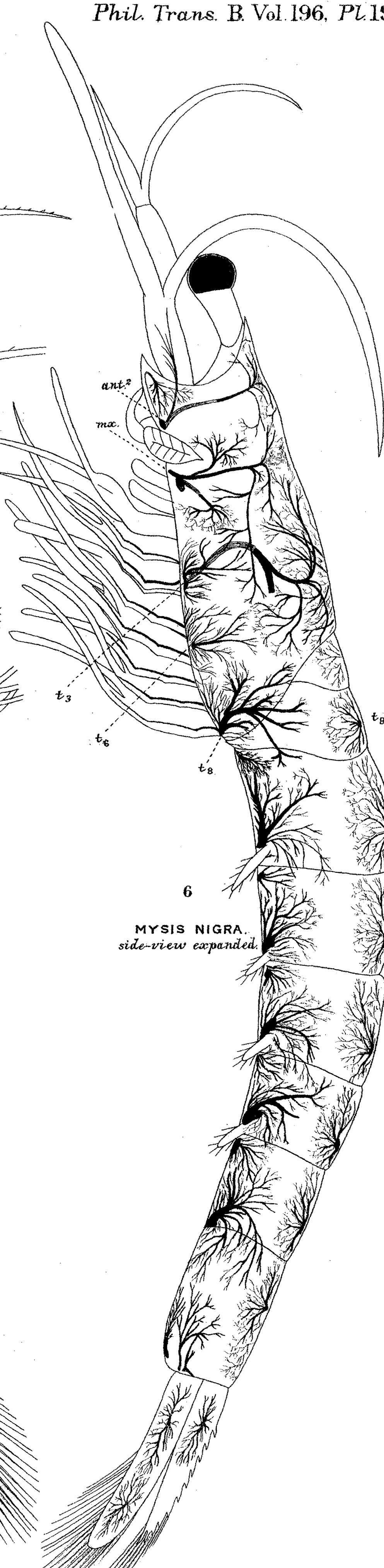
4

MYSIS NIGRA.
ventral half-expanded.



5

MYSIS NIGRA.
ventral expanded.

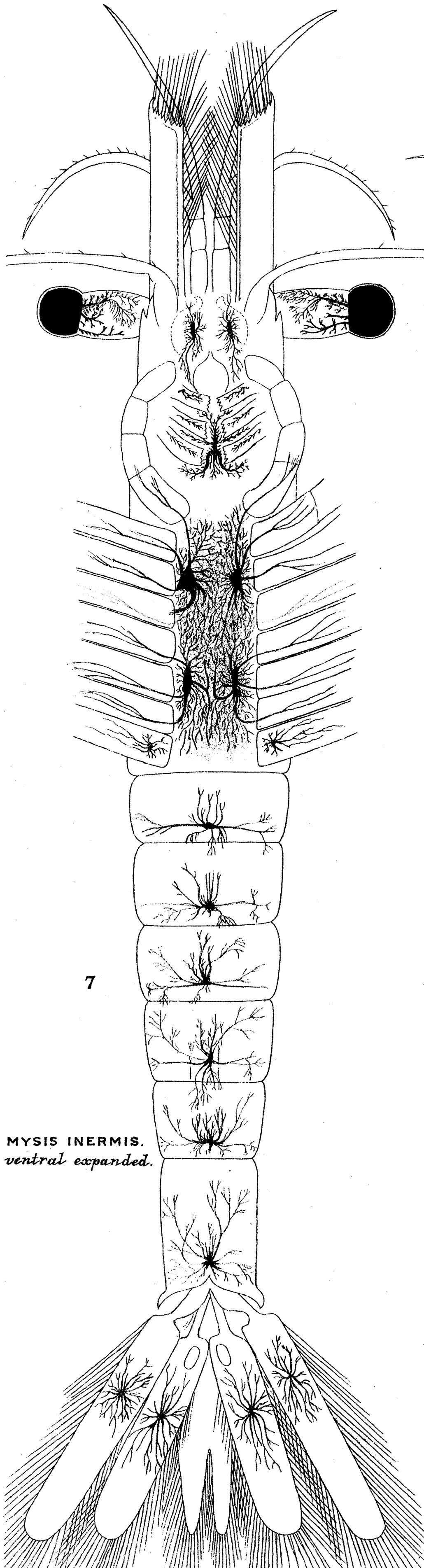


6

MYSIS NIGRA.
side-view expanded.

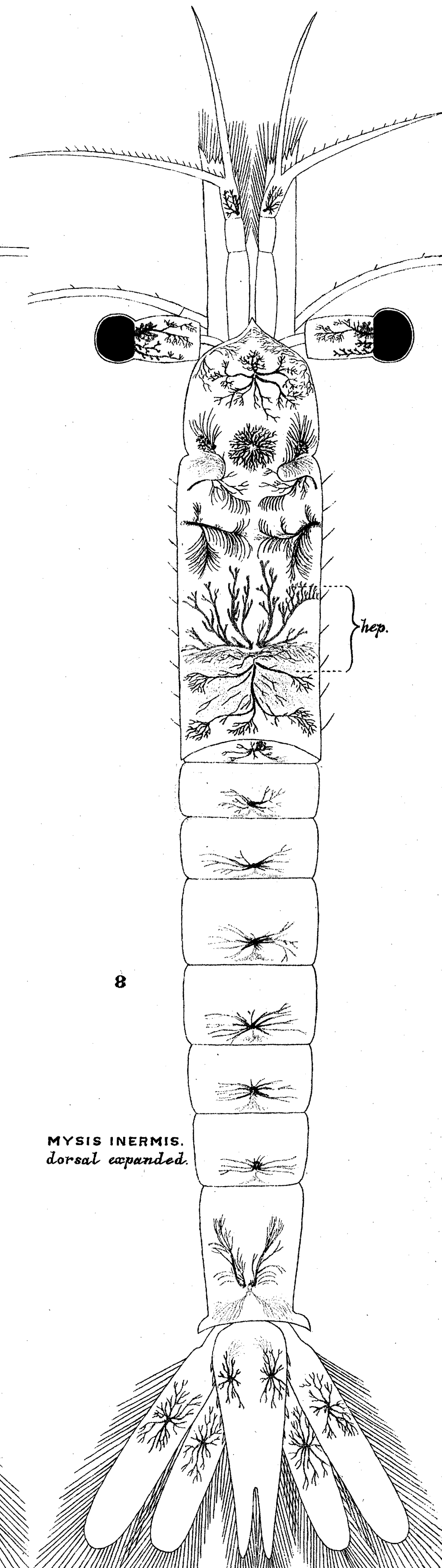
Miss D. Richardson del.
M.P. Parker lith.

Parker & West imp.



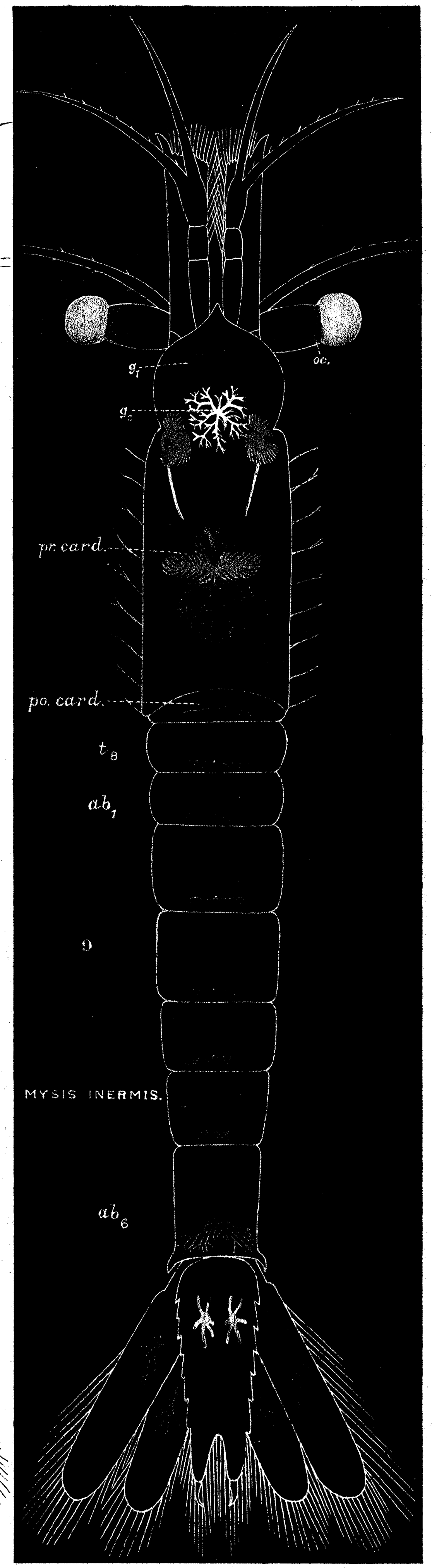
7

MYSIS INERMIS.
ventral expanded.



8

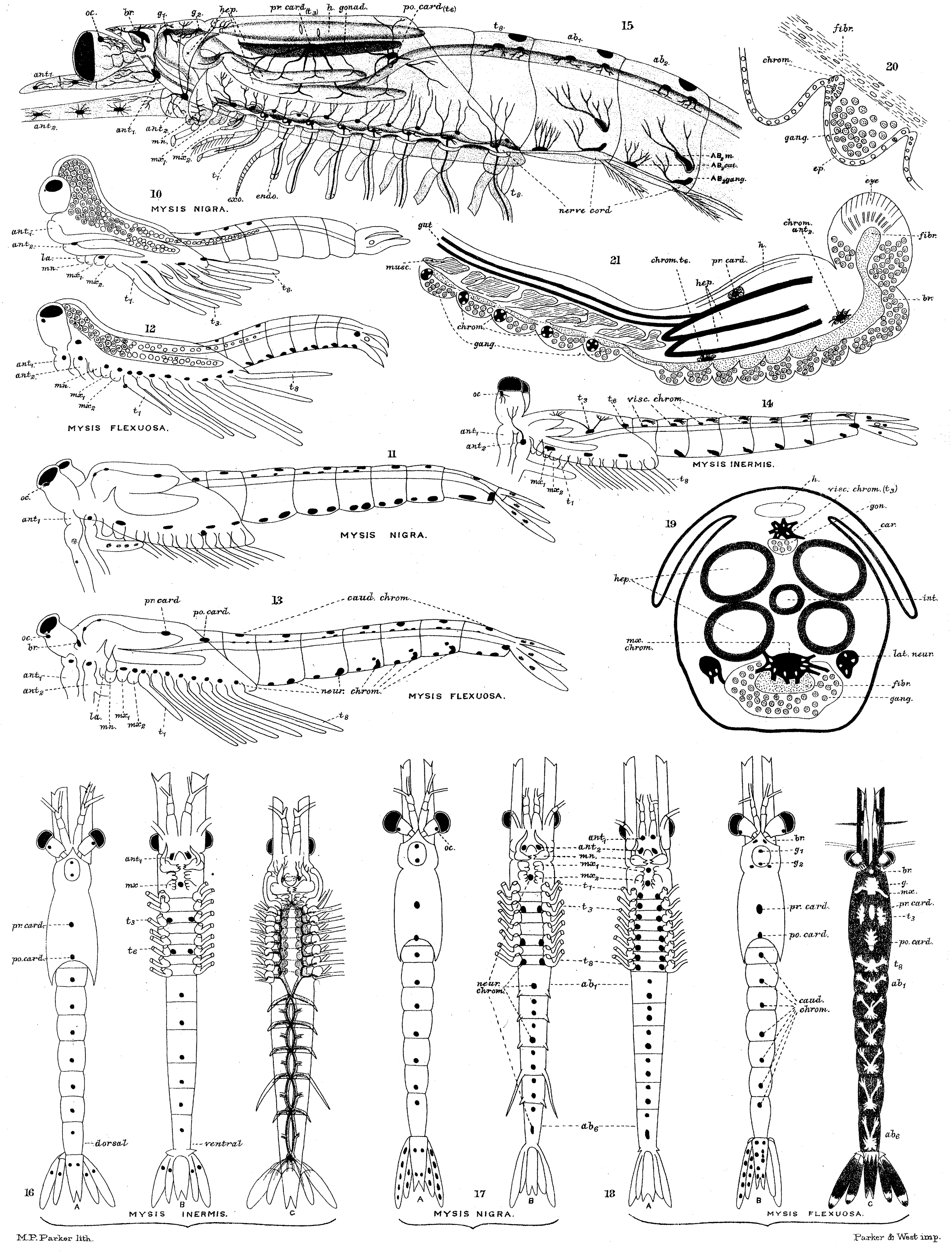
MYSIS INERMIS.
dorsal expanded.



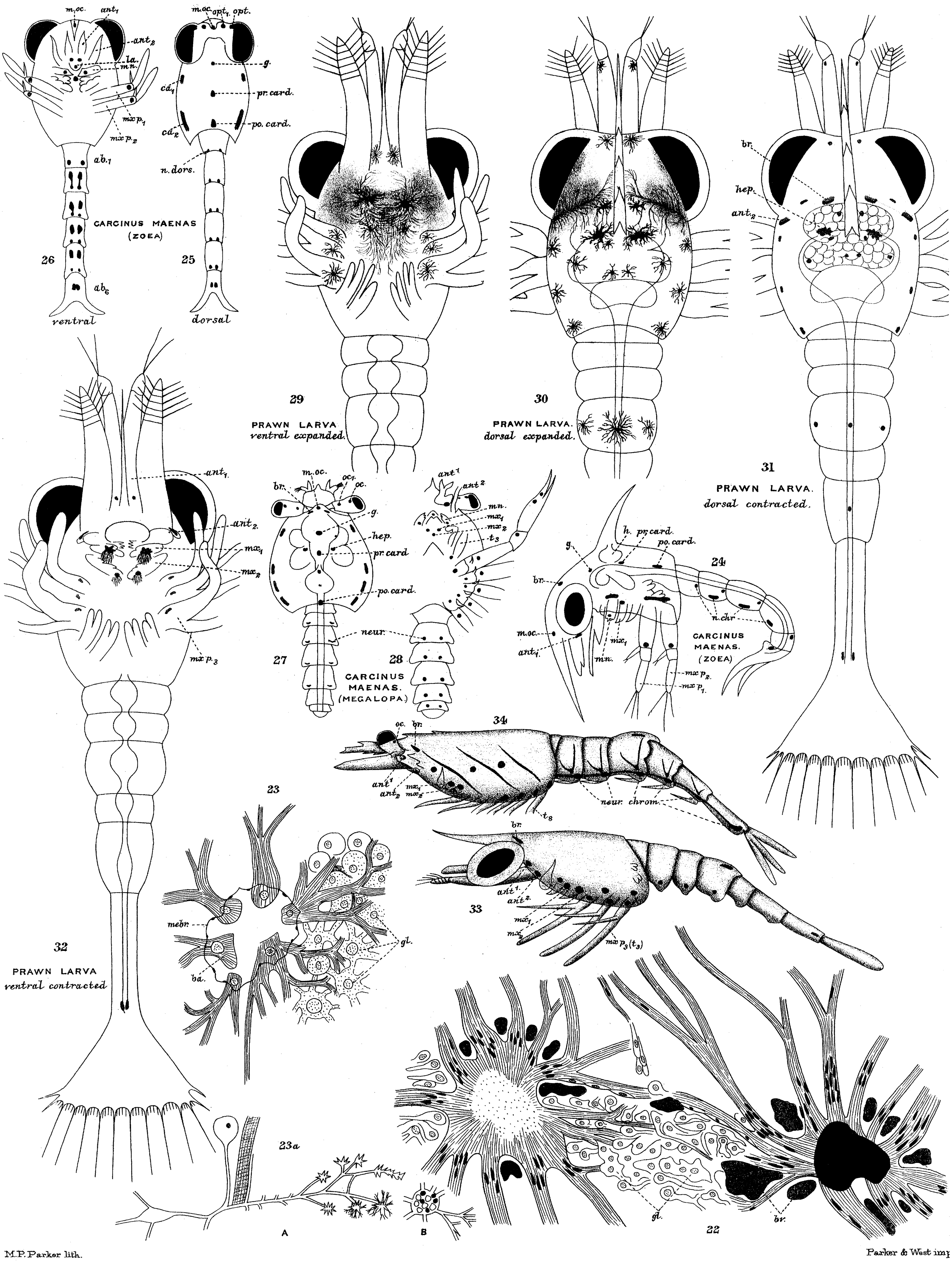
9

MYSIS INERMIS.

Miss D. Richardson del.
M. P. Parker lith.
Parker & West imp.

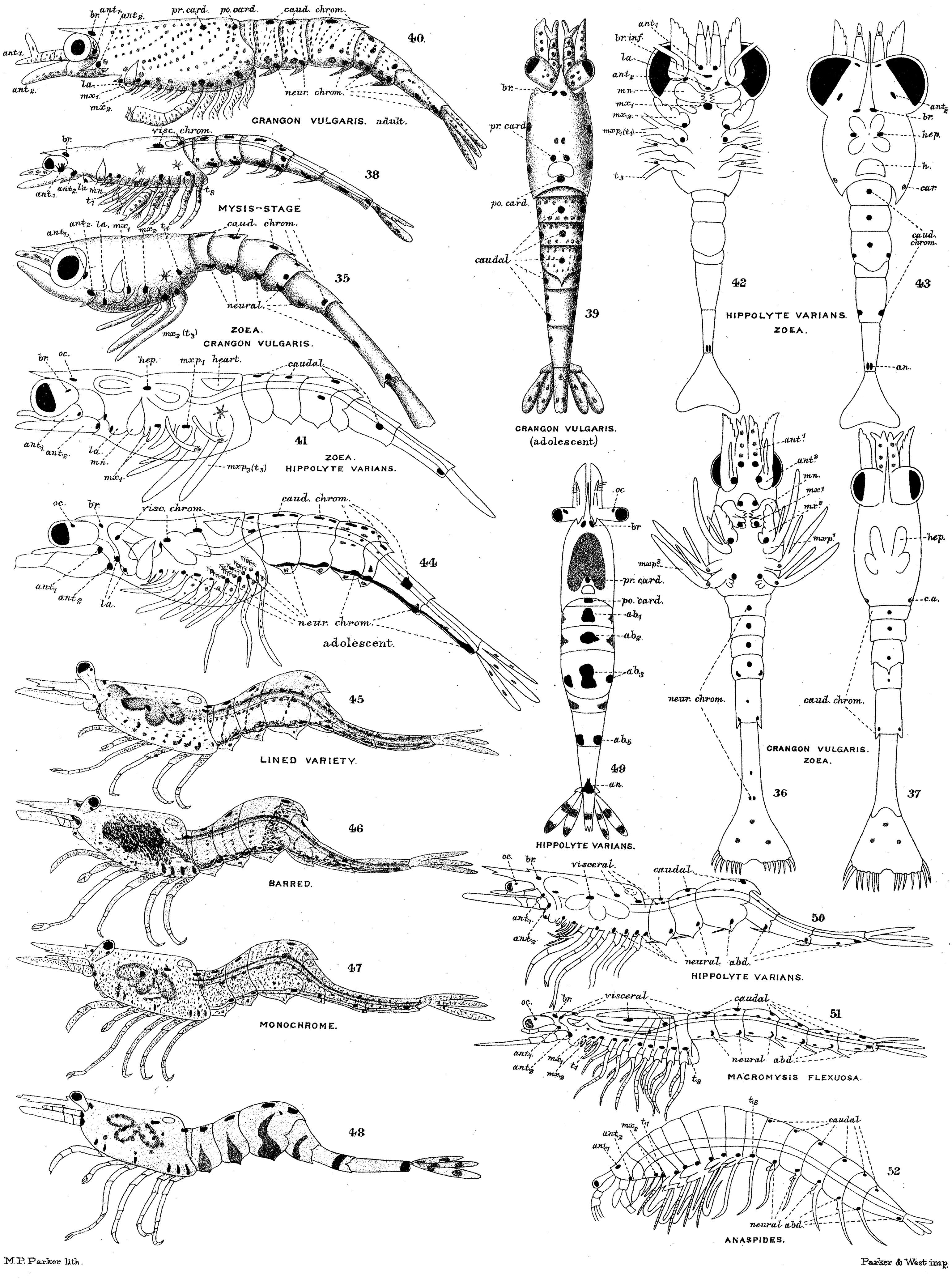


M.P. Parker lith. Parker & West imp.



M.P. Parker lith.

Parker & West imp


40.
br.
ant.1
ant.2
pr. card.
po. card.
caud. chrom.
la.
mx.1
mx.2
neur. chrom.
CRANGON VULGARIS. adult.
38
visc. chrom.
mn.
t1
t8
MYSIS-STAGE
35
caud. chrom.
neural
mx3 (t3)
ZOEA.
CRANGON VULGARIS.
41
oc.
hep.
mxp1
heart.
caudal
mxp3 (t3)
ZOEA.
HIPPOLYTE VARIANS.
44
visc. chrom.
neur. chrom.
adolescent.
45
LINED VARIETY.
46
BARRED.
47
MONOCHROME.
48
39
pr. card.
po. card.
caudal
CRANGON VULGARIS.
(adolescent)
42
br. inf.
mxp1(t1)
t3
43
hep.
h.
car.
caud. chrom.
an.
HIPPOLYTE VARIANS.
ZOEA.
49
ab1
ab2
ab3
ab5
HIPPOLYTE VARIANS.
36
37
mxp.1
mxp.3
c.a.
neur. chrom.
CRANGON VULGARIS.
ZOEA.
50
visceral
neural
abd.
HIPPOLYTE VARIANS.
51
MACROMYSIS FLEXUOSA.
52
ANASPIDES.

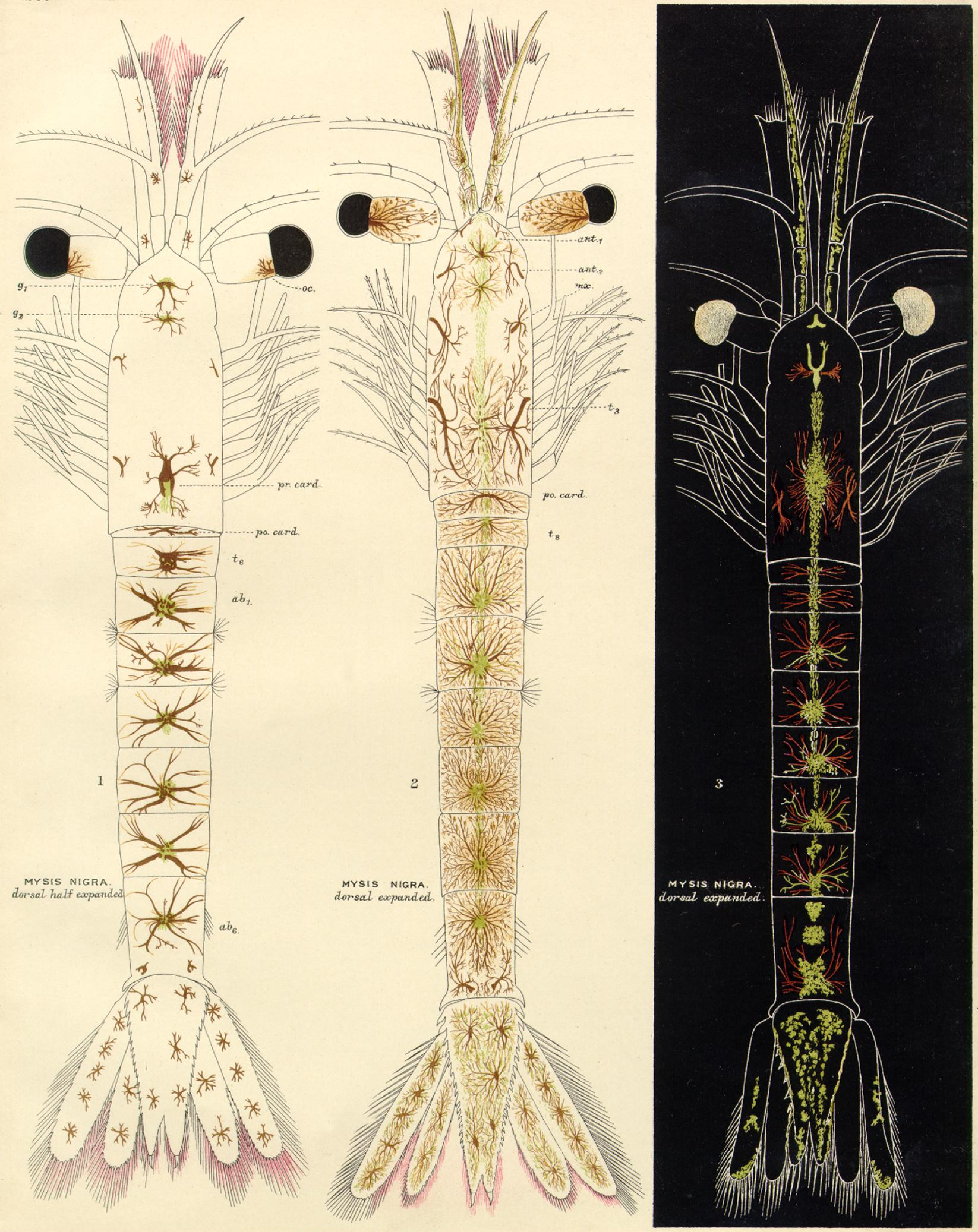


Plate 18 (× 15).

Fig. 1. *Macromysis nigra* n. sp. Dorsal surface seen with the pigment contracted.

Fig. 2. The same seen with the pigment and reflecting substance fully expanded. The figure shows the typical form of branching of Mysidean chromatophores, especially the long branches from the neural centres (Mx_1, T_3), and the branches on the optic stalk (Oc.).

Fig. 3. The same to show the reflecting substance on a dark background. In this species it does not assume a definite pattern. Contrast with *M. flexuosa*, Plate 21, fig. 18c, where the definite pattern is expressed.

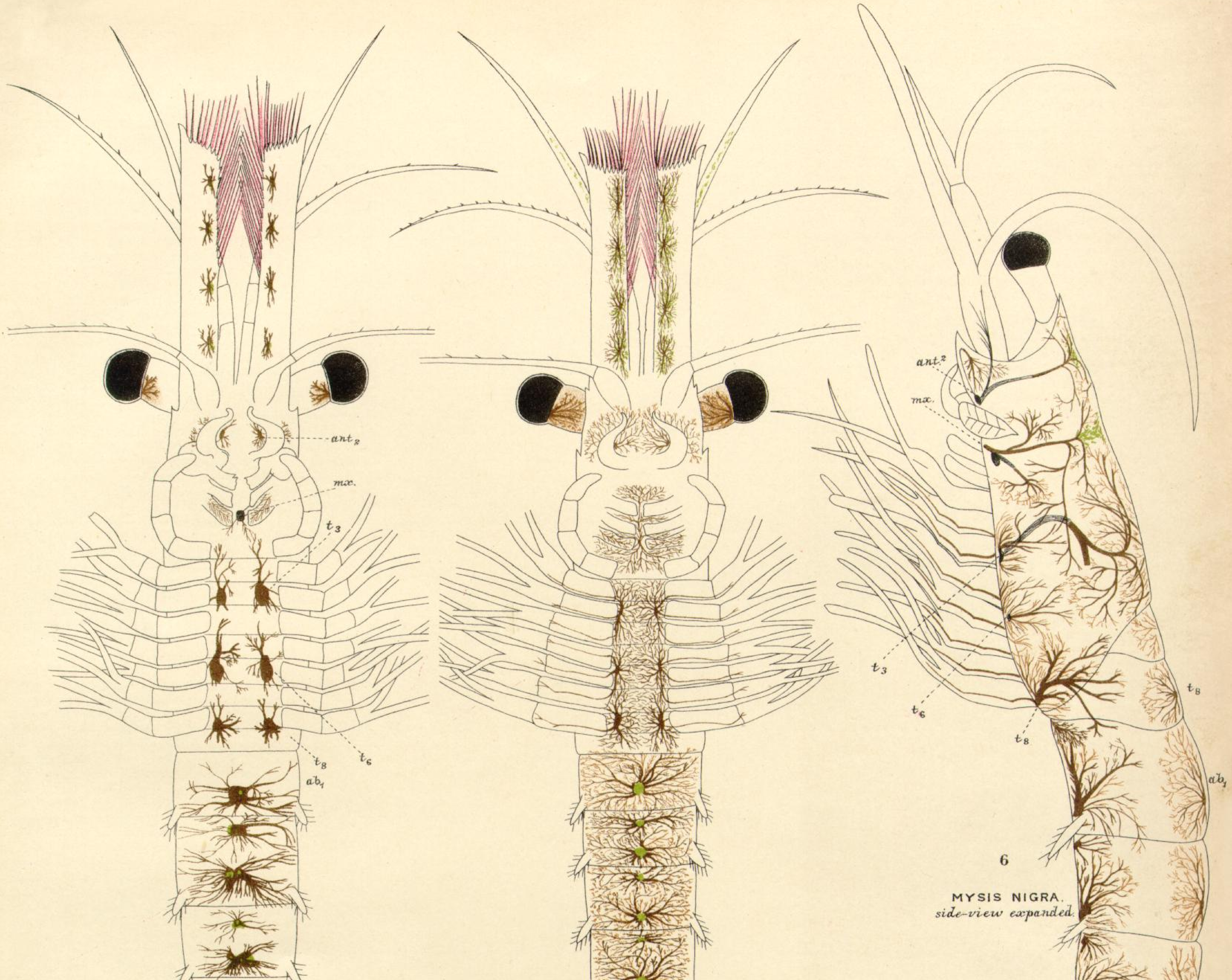


PLATE 19 (× 15).

Fig. 4. *Macromysis nigra* n. sp. seen from the ventral surface with the pigment contracted.

Fig. 5. The same with the pigment expanded.

Fig. 6. Side view to show the elaborate branch-system of the neural chromatophores that supply the carapace and skin, and the branches of the caudal centres (A, B_1, etc.).

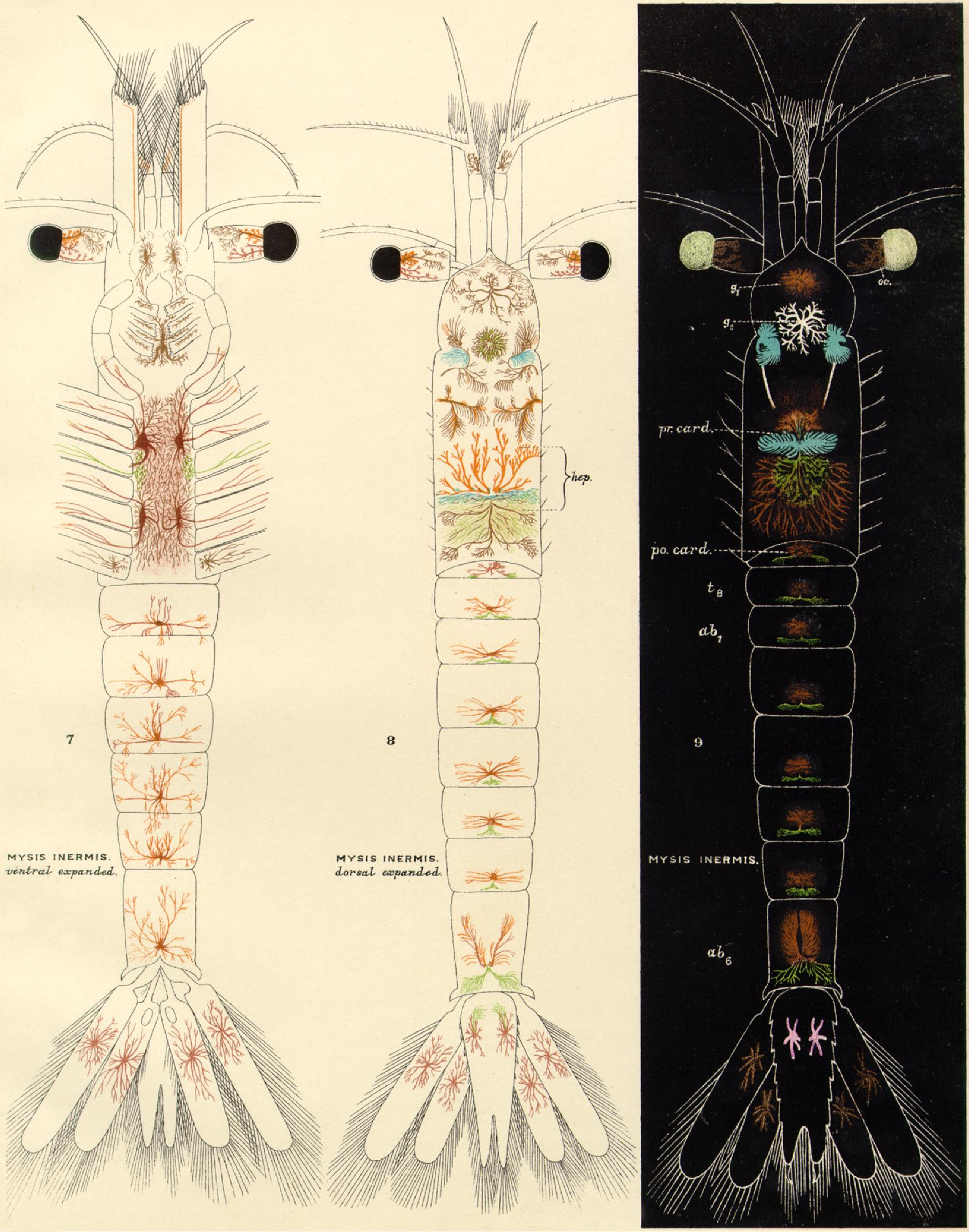


Plate 20 (× 18).

Fig. 7. *Macromysis inermis.* Seen from the ventral surface with the pigment expanded (compare with Plate 21, fig. 16). The relation of the branches to the nerve-cord and its nerves is very clear.

Fig. 8. The same from the dorsal surface. The figure shows the visceral branch system on the stomach, and especially on the liver and gonad (Hep); also the branches from the neural centres near the rostrum, and at the sides of the carapace. The form of the abdominal caudal chromatophores is very constant, and each one contains greenish-yellowish reflecting substance arranged in branches as shown. The arrangement of blue spots over the liver is quite constant and due to branches from the hepatic median centre, Hep.

Fig. 9. *Macromysis inermis.* Dorsal surface to show the definite and characteristic colour-pattern of reflecting substance on a dark ground. The branch-system of the second gastric centre, the large pre-cardiac (Pre-card) or hepatic centre, and each abdominal centre, is provided with a supply of reflecting substances: white, blue, greenish-blue, and yellow. The total effect in life is one of great brilliancy.

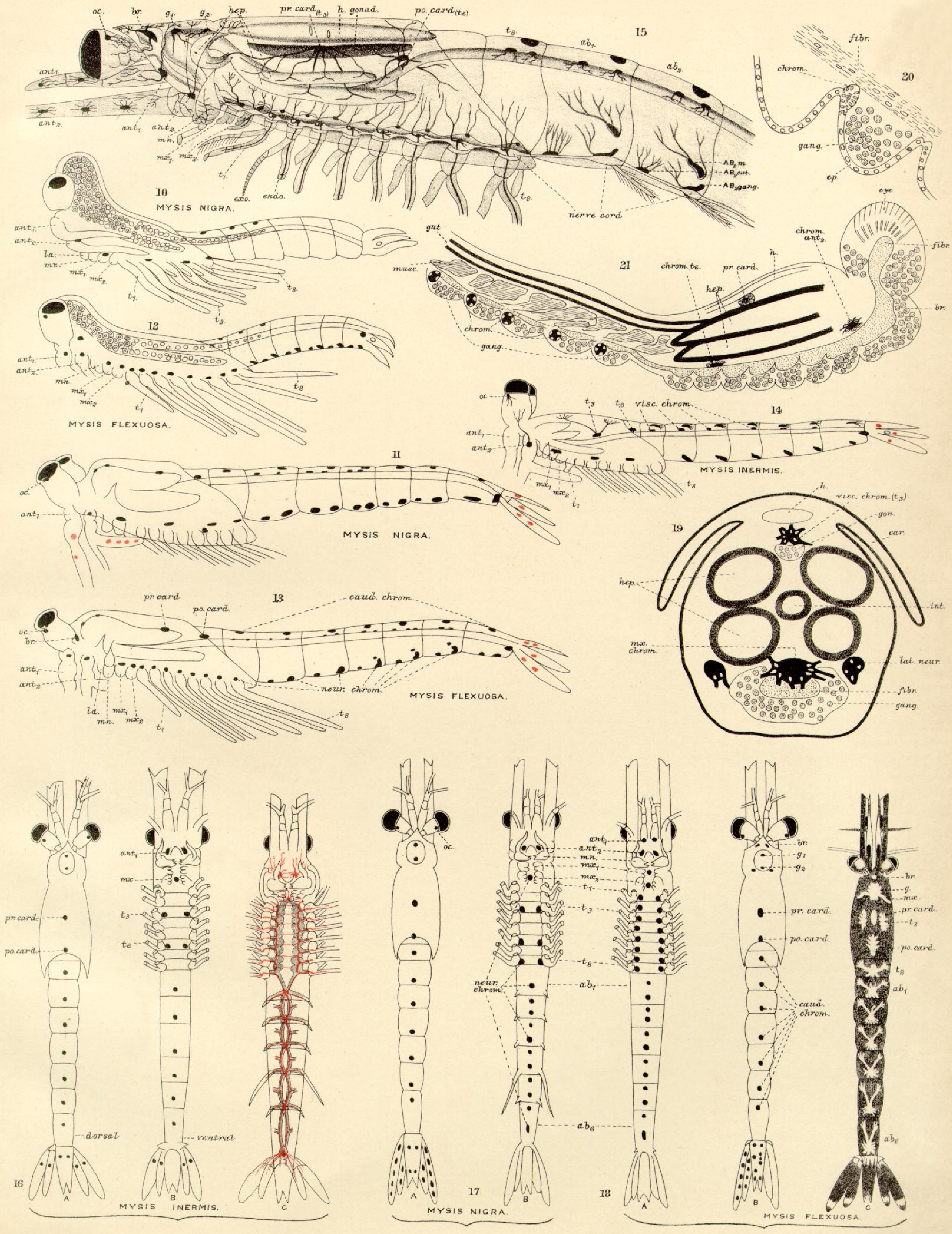


PLATE 21.

Figs. 10–14 are embryos of three species of *Macromysis*: the figures show that the characteristic arrangement of the chromatophore-centres is attained before birth. The specimen here called *Macromysis nigra* is when mature, but not full-grown, identical with *M. neglecta*. Subsequently when full-grown it assumes appendicular characters identical with those usually given as diagnostic of *M. flexuosa*. Hence we have had to adopt neither of the names *neglecta* or *flexuosa*, and have given this *Mysis* a new name (*Nigra*). Its characteristic features are the possession of neural centres on T_3, T_6 and T_8, and double abdominal centres (see pp. 331, 332).

Figs. 10, 11. *Macromysis nigra* n. sp. Figs. 12, 13. *M. flexuosa*. Fig. 14. *M. inermis*.

Fig. 15. Side-view of the anterior portion of the body of *Macromysis flexuosa*. The figure is drawn from a moderately expanded specimen, and shows both the centre-system and the branch-system. The neural centres extend from BR to AB_2 Gang., and together with the appendages indicate the number of segments. G_1, G_2, Pre-card, Post-card and Int, are the visceral centres; T_8, Ab_1, &c., are the caudal ones. The relation of the branches of the large pre-cardiac centre to the gonad and liver-lobes is well-shown. This feature is common to the majority of Mysidæ. To a less degree, the post-cardiac visceral centre supplies the same organs, and the hinder border of the carapace in addition. Compare the text pp. 302, 303. × 10.

Figs. 16–18. Dorsal and ventral views of three species of *Mysis* (or *Macromysis*) to show their constant adult chromatophore-characters. By the aid of these figures it is easy to identify specimens. × 4.

Fig. 16C shows (in red) the extraordinarily close relation of the chromatophores to the nervous system. Fig. 20 is to be compared with fig. 16B to show the change which expansion and contraction of the pigments makes in the appearance of the animal.

Fig. 18C shows the distinctive colour-pattern of *M. flexuosa* which is due to the reflecting substance constantly expanding into the same channels and causing the same arborisations to appear.

Figs. 19–22 illustrate the structure, development and arrangement of the chromatophores of *Macromysis flexuosa* and *M. inermis*.

Fig. 19. A diagrammatic transverse section across the embryo of *Macromysis flexuosa* to show the relation of two of the three chief groups of chromatophores—neural and visceral—to the nervous system and other organs. The white dots in the chromatophores are the nulcei. The section is taken across the antennæ and maxillæ.

Fig. 20. Vertical sagittal section of three ganglia in *Macromysis flexuosa* (embryo 2 millims. long), to show the mode of origin of the abdominal neural chromatophores as sacs developed at the expense of the epidermis covering the ganglia. For the significance of this mode of origin, see the text, Section II., p. 305, and Section VII., p. 333.

Fig. 21. Vertical section (a little to one side of the median line) of an embryo of *Macromysis flexuosa*. The figure is intended to show the relation of the developing abdominal neural chromatophore-centres to the embryonic ganglion cells. The nuclei are indicated by white dots.

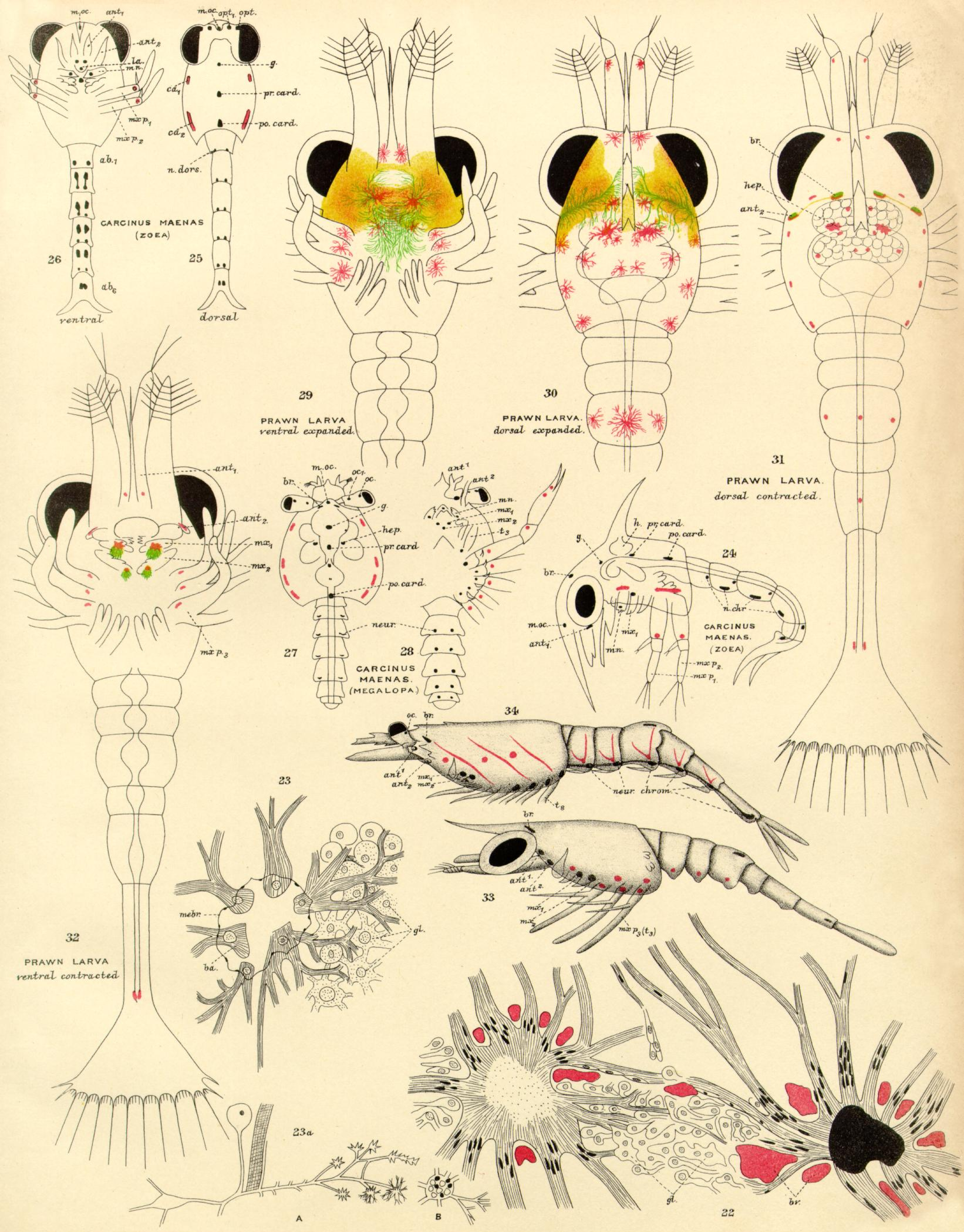


PLATE 22.

Fig. 22. Two chromatophores and intervening glandular and vascular tissue from the brood lamellæ of *Macromysis inermis*. In one, pigment has been left at the centre. Compare the text, Section III., p. 308, and Section VII., p. 333.

Fig. 23. A chromatophore from the telson of *Macromysis flexuosa*. The figure shows the apparent independence of the constituent cells, the way they are inserted into the central sac (*Membr*), and their fibrillar structure. The glandular tissue (Gl) which is so constantly associated with the chromatophores and their branches is shown.

Fig. 23A. A "chromatophore" from the musculature of *Hippolyte varians* to show the peculiar endings.

Figs. 24–28 illustrate the development of the chromatophores in the crab.

Fig. 24. The zoea of the common shore-crab (*Carcinus mænas*) seen from the side, to show the primary and secondary chromatophore-systems. It may be usefully compared with fig. 35. × 50.

Figs. 25, 26. The zoea of the shore-crab *Carcinus mænas* before its first moult, seen from above (25) and from below (26). The neural centres are very strongly developed, and in the abdomen are not only paired, but send upwards a process which becomes virtually isolated (*N. dors*), and appears in the dorsal view. The secondary system is composed of two pairs of carapace-centres and of maxillipedal ones. These figures are to be compared with figs. 42 and 43, the zoea of *Hippolyte*, and still more instructively with *Mysis*, Plate 21, fig. 18. × 50.

Figs. 27, 28. The "*megalopa*-stage" of the shore-crab (*Carcinus mænas*) from the upper (27) and under (28) surfaces. The figures show that in spite of the alteration in form and complexity as compared with the zoea, the crab has retained the zoeal chromatophore-system, and has merely subdivided the secondary chromatophores on the carapace: thus the primary system is not concealed as in *Hippolyte*, or *Crangon* by the secondary one, at least during the contracted phase. Later on, the individual centres of both systems merge into a sheet or double sheet of superficial inert masses. It will be noticed that the caudal group of primary chromatophores is absent (*cf.* text, Section IV., pp. 317–319). × 15.

Figs. 29–33 are drawings of the zoea-larva of *Palæmon squilla* showing dorsal and ventral views both of the expanded and contracted pigmentary phases. × 50.

Fig. 29 shows the two pairs of maxillary centres, with their elaborate branches of red pigment and green reflecting substance. The former branch up dorsally into the nervous tissues, and give rise to the splash of orange colour seen in the figure.

Fig. 30 shows the same animal from the upper surface. The splash of orange colour is seen through the optic ganglion. Along what will eventually be the frontal margin of the carapace, is an arborescent green marking due to the branches of both the supra-cerebal centres (Br) and of the deep antennary centres (Ant_2). The three pairs of centres on the carapace form the beginnings of the characteristic stripes of the adult. (See fig. 34.) There are three pairs of small hepatic centres and one pair of large ones (Hep).

Fig. 31. The dorsal surface of the same larva with the pigment contracted and the centre-system very distinctly shown. The anal chromatophores are the only neural centres present in the abdomen at this stage.

Fig. 32. The ventral surface showing the centres of the neural group of chromatophores; to be compared with fig. 29.

Figs. 33, 34 show the origin of the characteristic colour-pattern of *Palæmon squilla* from its zoea-pattern. These figures also show how the neural primary group of chromatophores is developed in the late larval stage as in *Hippolyte*, and not in the early larva as in *Crangon*. The persistence of the large neural maxillary centres of the larva is also shown. The visceral system of chromatophores is omitted (fig. 34). × 12.

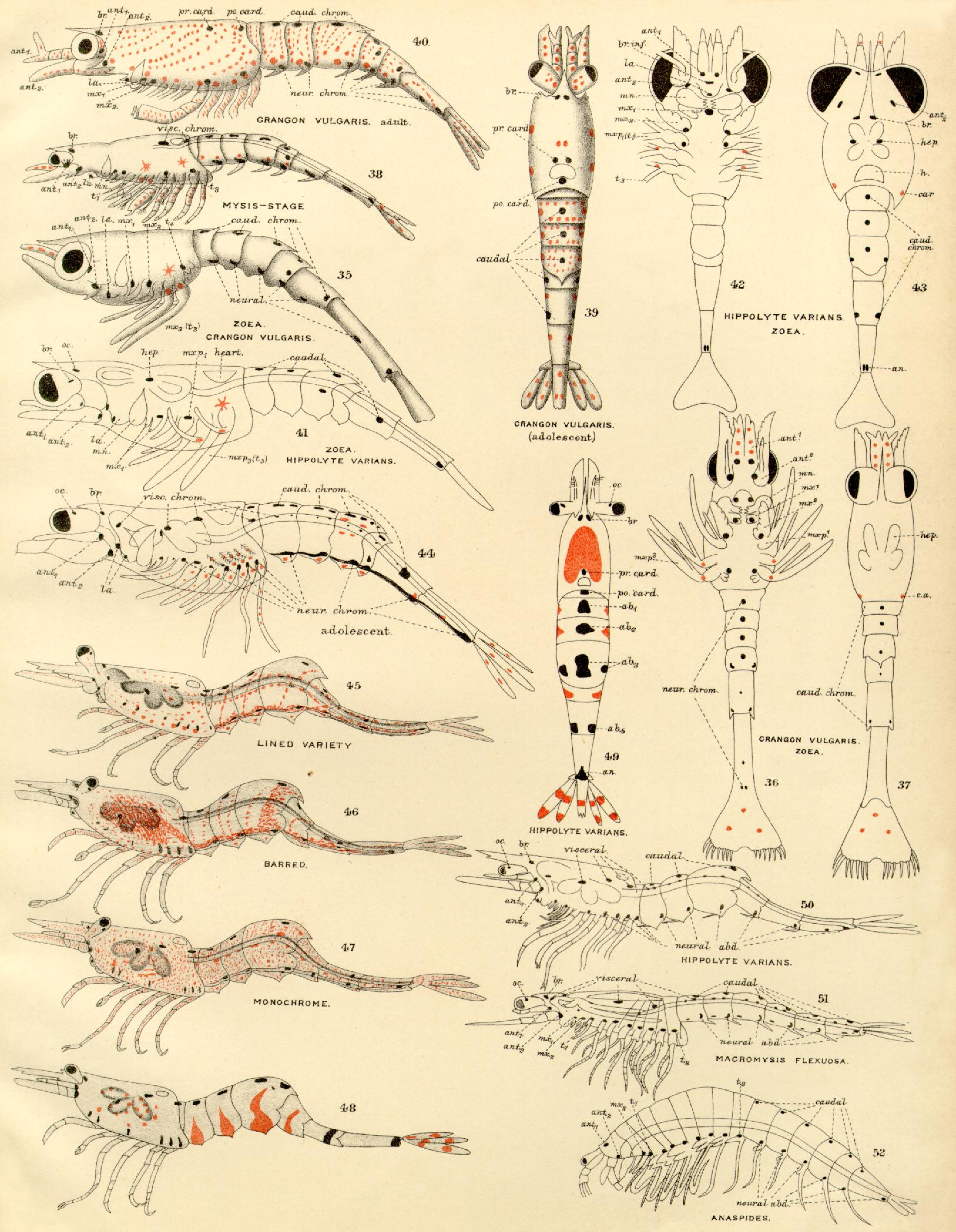


PLATE 23.

The figures on this plate illustrate the development of the primary and secondary systems of chromatophores in the Shrimp (figs. 35–40) and in *Hippolyte varians.* The former system is coloured black, the latter red. For the actual colouring see the text (Section IV.).

Fig. 35. The zoea of the Shrimp (*Crangon vulgaris*) seen from the side. The primary centres are for the most part median, and some paired. Which are median and which are paired can be determined by reference to figs. 36, 37. × 43.

Figs. 36, 37. Zoea of the common Shrimp (*Crangon vulgaris*) to show the primary chromatophore-centres (black) and the secondary ones (red). These figures are to be compared with the views of *Mysis*, particularly *M. inermis.* Plate 21, fig. 16. Fig. 36 is the ventral view. Fig. 37, the dorsal one. × 40.

Fig. 38. Late-larval ("*Mysis*-stage") stage of the Shrimp. The figure shows that additions have been made both to the primary and secondary systems of chromatophores. The visceral centres (*Pre-card* and *Post-card*) have now appeared. × 15.

Fig. 39. Adolescent stage of *Crangon vulgaris* from a specimen 5 millims. in length. Dorsal view to show the manner in which the secondary system of chromatophores (red) arise on the carapace and pleura, and also the persistent primary caudal and visceral centres (black).

Fig. 40. Adult stage of *Crangon vulgaris* to show the relations of the primary and secondary systems of chromatophores. The former persists as well developed neural and caudal groups, but as a reduced visceral group.

Figs. 41–49 illustrate the development of the colour-pattern of *Hippolyte varians.*

Figs. 41–43. The zoea of *Hippolyte varians* to show the primary and secondary chromatophores, the former in black, the latter in red. The centre-system of this larva, like that of the larvæ of the other Decapods we describe, is perfectly constant. Each centre contains a red pigment and yellowish-green reflecting substance. When expanded into the branch system, filmy stellate patches are produced over the head, carapace and tail, and on the appendages and nerve-cord. By reflected light these patches appear greenish-white; by transmitted light they have merely a greyish tint. × 80.

Fig. 41 lateral view, fig. 42, ventral view, fig. 43, dorsal view.

Figs. 44–49 are intended to show how the three chief adolescent colour-patterns of *Hippolyte varians* are derived from the single and uniform pattern of the larva. (*Cf.* the text, Section V., pp. 324–328.) × 30.

Fig. 44 is an early adolescent phase (4–5 millims. long), and is a phase passed through by many, if not by all *Hippolyte varians* on their way to more distinctive patterns. The neural system is now complete, the visceral system is well-developed, and a secondary series of centres (red) have been developed in the carapace, at the bases of the gills and legs, and on the pleura of the tail. When expanded, this centre system gave the appearance of a faint brown-liner. Much of the reflecting substance of the larva is still present.

Fig. 45 shows how by hypertrophy of the intestinal visceral centres, and by the formation of secondary centres below the gut, across the tail-segments, around the liver and on the carapace, the "liner" colour-form is produced. It may be red, yellow, green or brown, with bars and spots of superficial reflecting substance.

Fig. 46 shows how by hypertrophy of secondary centres round the roots of the great vessels, the liver and gonad, a bar of colour is formed in the thorax; by increase in the number and size of the elements in the third segment of the tail, a second bar is formed. Thus the "barred" colour-form arises.

Fig. 47 shows how by the development of minute chromatophores scattered evenly in the muscle, on the viscera, nerve-cord and skin, one type of "monochrome" colour-form arises.

Fig. 48. Side view of the blotched colour-variety. The importance of this colour-form lies in the fact that it is based on an underlying "liner" pattern seen in fig. 45, and that it occurs in other species of Crustacea, for example in *Hippolyte cranchii* and *H. pusiola.* (See the text, Section V., p. 324.)

Fig. 49. Dorsal view of the "blotched" colour-form of *Hippolyte varians*, showing that the primary system may give rise indirectly to a part of the colour pattern, which in this case is formed in a very definite and segmental manner. Round the liver, on the carapace and pleura, bands of chromatophores arise.

Figs. 50–52 are side views of *Hippolyte varians* (primary system of adolescent-stage), of *Mysis flexuosa* and of *Anaspides.* A comparison shows that the neural group of chromatophores occurs in all three animals at the base of the appendages; that a more restricted visceral group occurs in the *Hippolyte* and *Mysis* (*Pre-card*, *Post-card* and G_1, G_2); and that a caudal group occurs in all three genera.

The importance of *Anaspides* is referred to in the text (see p. 330), and it is introduced here to show diagrammatically how its chromatophore-system may be compared with that of *Mysis* and *Hippolyte.*